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ULF BERGSTRÖM

Observations on Norwegian lemmings,  
*Lemmus lemmus* (L.), in the autumn of 1963  
and the spring of 1964

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**Observations on Norwegian lemmings, *Lemmus lemmus* (L.),  
in the autumn of 1963 and the spring of 1964**

By ULF BERGSTRÖM

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## Introduction

In September 1963 reports were received at the Swedish Museum of Natural History from the province of Jämtland that from the late summer and onwards, Norwegian lemmings had been moving down from the mountains and were being encountered in the woods and the farmland at greater or lesser distances from their breeding grounds. In order to make observations on this migration, the author went up to visit some localities specially mentioned by the informants. The time 24th September–9th October was thus spent in the district around a farm called Sundet, and later, opportunities arose for two short visits to another locality, Hammarnäset, later in October. The migration also involved Härjedalen, the adjoining province to the south, which, however, was not visited until the spring. During this trip, between the 14th and 23rd of May, visits were paid to the same localities as in the autumn, and to some mountain districts as well.

### The localities mentioned in the text (see map)

In the text, a *fell* is used to denote a mountain area reaching above the tree-line. The normal breeding grounds of the Norwegian lemming are to be found both above this limit on the tree-less fell plateaux and below it in the adjoining subarctic (subalpine) birch wood zone. Contrary to higher up in Lapland, in Härjedalen and Jämtland this birch wood belt is generally very narrow so that the conifer woods at many places stretch up near to the very fell plateaux.

Lake Storsjön is situated in the middle of the province of Jämtland, with the town of Östersund on its eastern bank. Between the Norwegian border and this lake, there is an extensive water system, stretching in the general direction from NW to SE. It is mainly composed of three big lakes, of which Lake Kallsjön is one. Below this lake and after the conjunction with another broad river from the west at Järpen, the water system continues in the form of smaller lakes and streams and finally empties into an inlet which cuts deeply inland from the NW part of Storsjön. The inlet forms the southern side of a peninsula, Hammarnäset, which protrudes into the lake in a SE direction.

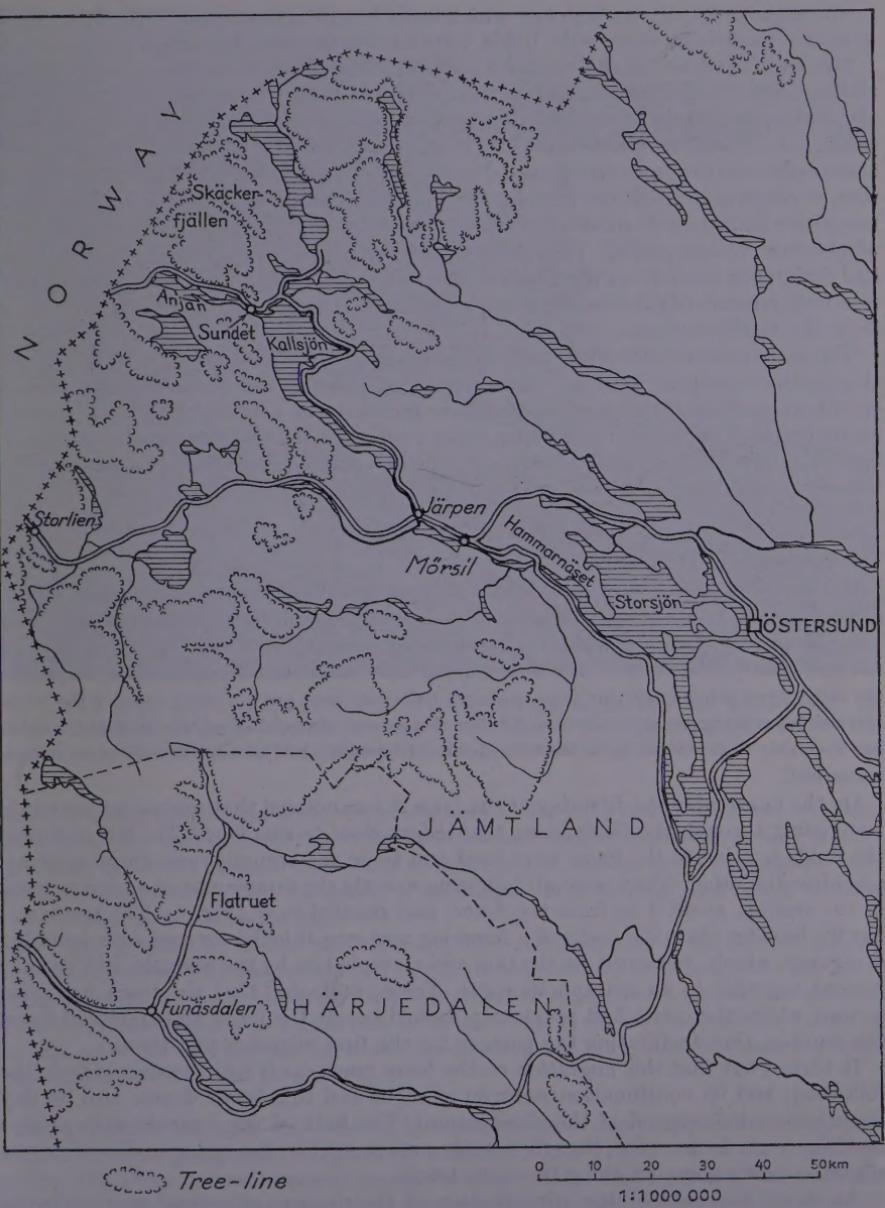
After rounding the northern end of Lake Storsjön, the main road north from Östersund runs westwards. When it meets the water system it passes a place called Mörsil and follows the north side of the water up to Järpen. Here the road crosses the river and, continuing to the west on the north side of the adjoining river, finally crosses the Norwegian border at Storlien, which is situated within a fell district that lies on both sides of the border. At Järpen another road branches off to the north, following first the east side of the river coming from Kallsjön and then the lake shore up to the northern end. From there the road continues to the west, passing the farm Sundet and another lake, Anjan.

In Härjedalen, a fell area called Flatruet, about 30 km NE of the village of Funäsdalen, was visited in the spring. On leaving Funäsdalen, the road between Härjedalen and Jämtland goes first towards the east, then turns towards the north and after passing along the western side of Lake Storsjön ends at the main road from Östersund to Järpen. While driving along the roads mentioned counts of run-over lemmings were made, which gave some indication of what movements were going on in the vicinity.

## I. The autumn observations

### Observations in the area around Sundet

In the autumn, most of the time was spent on observations of the lemmings in the fields of Sundet and its surroundings. The migration was also observed at other places



Map of the districts mentioned in the text.

in the area, i.e. along the highway which leads from the north end of the Lake Kallsjön and, passing just above the fields, continues to the west past another lake, Anjan.

Sundet is situated in the conifer woodland about 7 km from the nearest fell area to the north, Skäckerfjällen, and on the north side of an arm of Lake Kallsjön. From the northwestern part of the lake, this arm stretches to the west. At its end the water pours out of Lake Anjan in a rapid stream. Below Sundet the arm has already become rather narrow, measuring about 100 m across. Apart from the lemmings actually seen wandering through the area or just making a temporary rest for feeding, there was also a considerable number of other, stationary lemmings to be found during the whole observation period. Though obviously all the animals here in the woodland had emigrated there from the fell districts, in the following text for the sake of brevity only animals of the first category are referred to as migrants, to distinguish them from the stationary ones.

The daily contact with the lemmings gave opportunity of studying how the migration in the woodland appears when it goes on through the country under normal conditions, without the more spectacular incidents in connection with accidental accumulations. It also revealed how, away from their natural haunts, the stationary lemmings here had adapted themselves to the new surroundings, and this aspect of the lemming migration has been found worth relating in some detail.

### *The migrant lemmings*

#### *The migration in the fields*

The fields of the farm sloped down towards the shore with their lower borders stretching parallel to the shore-line in an east-west direction. Between the borders of the fields and the water there was a steep slope of varying height, for the most part covered with a dense vegetation of coarse tall grasses and herbs, but here and there showing naked sand scars of erosion slides. To prevent the cattle from going down this slope, a simple fence had been put up along some of the fields. It consisted of an upper row of laths and below this several rows of barbed wire so that the cattle had been able to graze just up to the fence but not beyond it, thus leaving the vegetation outside untouched.

On the morning of the first day at the farm it was noticed that migrating lemmings were going through the fields along their edges close to this fence. The last metres of the fields just inside the fence were level and there the animals came running along, one after the other. They were all following exactly the same route on a narrow track in the stubble about 1 m from the fence, and parallel to it (Fig. 1). The track was hardly broader than the body of a lemming and was thickly covered with lemming droppings which, wetted by the rain and trampled on by the animals, had become packed together to an amorphous paste. Traces indicated that the track had been formed where the cattle had previously walked beside the fence and trampled down the stubble, thus facilitating the passage for the first migrants just there.

It turned out that this migration on the fence track (as it will be referred to in the following) and its continuation went on at night and to a lesser degree also by day during the whole period of the observations. The bulk of the animals were always heading towards the west, though a weaker movement in the opposite direction was simultaneously going on along the same track.

As these migrants in the continuation of their course at several spots behaved unexpectedly as to their choice of route, this will here be described.

Having gone along the fence track to the west end of the fence, the lemmings had a hard-grazed grass area in front of them. Instead of proceeding onto this they all followed the track



Fig. 1. View to the east over the lower edge of some fields at Sundet with the "fence track". Of the two dark lines on the ground, the one next to the fence is the migration track made by the lemmings (the line to the left of this is the shadow of the fence).

which, following a slight depression, turned obliquely at that point and ended at the very edge of the slope. There they descended and disappeared into an entangled vegetation of coarse grasses, herbs and bushes. No common track could be detected here and the animals apparently went scattered along the slope. They reappeared at the further end of the grass area, mostly by using a path leading up to it from the water.

Here they switched to another path beginning there and continuing to the west, thus again parallel to the shore. This path started half way up the slope which from here onwards was much higher. It ran gently down, under the cover of a dense leaf-canopy which screened off the view of the water, until it ended on a small rock at the shore-line. It was only from the last metres of the path before this rock that one had a free view in front over a sandy stretch of shore beginning below it, and over the water beyond (Fig. 2).

The ground of the path was covered by a thick layer of dead leaves which was more resistant to trampling than the ground in the fields, for in spite of all the lemmings having run there, no well marked track was discernible. Also from the fact that the droppings were more scattered it was evident that the animals were using most of the width of the path.

On the first day, the observer happened to be standing watching the lemmings as they arrived at the end of this path (Fig. 2). It was then found that part of the

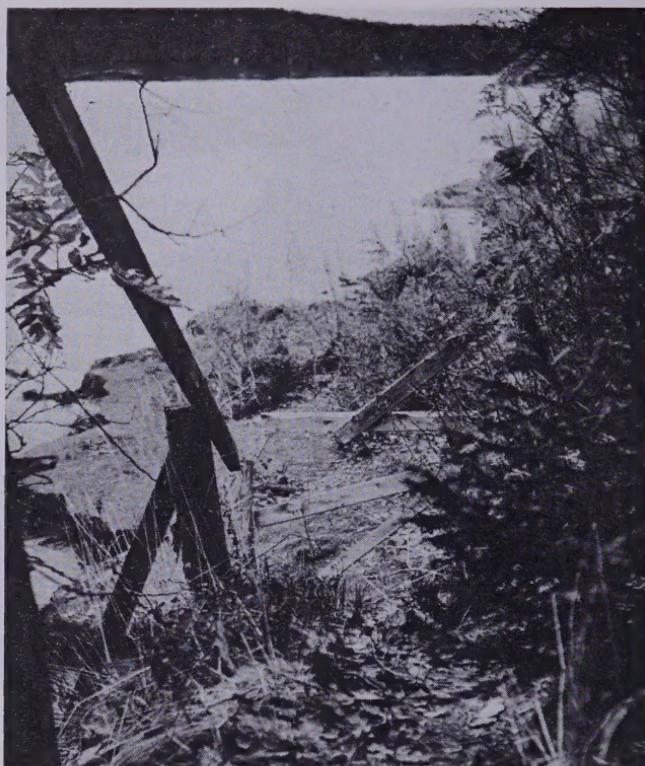


Fig. 2. The view at the end of the path used by the migrating lemmings, with the sand shore and water below in front (text, p. 325).

animals, instead of continuing to the rock, at exactly one and the same spot turned sharply aside and disappeared under some small spruce bushes growing on the land side of the path, just at the base of the slope from the field above (Fig. 4). The animals came running at their regular pace and the turn was made instantaneously without slowing down even for a fraction of a second. The same behaviour, with a varying percentage of the animals turning, would in the following time be witnessed on any occasion that the spot was visited, whether in daytime or by night.

Meanwhile, those lemmings that had continued straight on to the rock, by their subsequent behaviour evinced an obvious unwillingness to proceed any further that way.

One night it was observed how two animals, when arriving at the rock at once turned and quickly ran back a few metres along the path, dived into the grass on the shore side of it but immediately reappeared, crossed the path and disappeared under the spruce bushes. With the exception of these two, all the animals which took this route behaved in the following way:

They would linger hesitantly on the rock, walking to and fro and looking down over the edge, apparently not daring to climb down. This seemed strange, since



Fig. 3. A lemming running on the path (at the same place as in Fig. 2) and passing the spruce-bushes mentioned in the text (p. 326).

the height of the rock was only 1 m and there were shelves leading down to a strip of sand between the rock and the water. Once down on the shore they could have continued conveniently along it for quite a distance. Instead of this they began finally climbing along the slope, searching their way upwards in the dense vegetation until they arrived at one of the sandy erosion scars present there. In furrows in the middle of this they turned straight upwards, climbing laboriously in the sand until they reached the edge of the slope. Those animals that had turned earlier at the spruce bushes immediately started climbing diagonally until meeting with a scar and so arrived up as the others.



Fig. 4. Another lemming turning off just before the same bushes.

Above this slope there began a field in which the top-soil had been removed from a broad strip, from the edge inwards, so that the sand underneath could be exploited.

Up on this bare sand plateau the lemmings continued running towards the west and thus once more travelling parallel to the edge of the slope. Here each animal found its own way, only occasionally making use of truck-tracks leading in the same direction. Arriving at its further end, the animals had in front of them an uphill slope of sand. In the face of this, a sand pit had been dug out, which cut the face all the way up. The part of the rise that was left between the pit and the edge of the slope down to the shore formed the beginning of a rough road for the trucks. The road turned inland immediately behind the pit so that the upper edge of the pit was on one side of the road, while on the opposite side the ground ran steeply down into a little valley leading down to the water at right angles to the shore.

To reach the summit, part of the animals used the untouched side of the slope, but just as many went directly into the half-circle of the pit. The choice between these two routes was made independently of whether another lemming was within sight in front of them or not and was merely accidental, the animals not being able to discern from a distance the difference in steepness between the equally high parts of the rise. None of the animals that arrived within the pit made any attempt to avoid the steep sand wall in front by turning a few metres to the side and by doing so getting out of the pit again. They continued straight on and without hesitation started a difficult climb and at last found a spot where they could get up over the edge. They, too, were now on the road at about the same spot as the other animals who had arrived there conveniently by the truck road. Still keeping the same direction, all the animals now went down the steep slope of the valley and from its bottom climbed up the opposite tree-covered slope and disappeared into the forest behind. If they had instead followed the road from the plateau in towards land, or a path on the bottom of the valley, they could have proceeded on level ground across some fields further to the west.

Thus, while the same lemmings a while ago at the end of the path with the sand shore in front of them had turned away from this and taken a new direction at right angles, which involved a difficult and time-consuming climb, they here stubbornly went straight on, though a temporary deviation in towards land would have offered a much easier course.

It turned out that during the whole observation period the lemmings that came by the fence track and the path, constantly followed the same rigid pattern as to the details of their course described above.

The curious sight when some of the lemmings, running along the path suddenly turned off just before the spruce bushes as if pulled by a string, instead of continuing the remaining metres, seemed at first to suggest that this was induced by their sense of smell. Scent trails from previous lemmings which had likewise deviated could evidently be present there, leading up to the bushes. Considering, though, that the animals arriving at this point were not running on a narrow track but on a path which reasonably had scent trails across most of its width, it appeared, however, questionable whether they would be able in passing to perceive a scent trail that branched off. If this had been the case, they might have been expected at least to slow down when meeting with the two alternatives.

As an experiment, one night the leaf cover of the path some metres before the bushes was scraped off with a rubber boot for about a metre. The animals subsequently arriving at this spot did not slow down their speed in the slightest degree.

It therefore seems that it actually was the sudden view of the water in front that for some unaccountable reason had a deterrent effect that made part of the animals

turn off and take shelter in the vegetation at the side of the path. It was then natural for them to run up to the bushes, as these offered the best cover within reach. The event mentioned when two lemmings coming from the grass on the opposite side rushed across the path up to the bushes likewise indicated that the bushes themselves without the aid of a scent trail could attract intimidated animals. It might be mentioned that for a human observer even on overcast nights the water was visible as a light surface contrasting with the dark wood behind.

Still, the puzzling fact remained that the greater part of the animals chose to run straight on past the bushes without showing the slightest hesitation when confronted with the same view as the others, though they, too, soon after turned away from the shore-line.

Simultaneously with the migration on the fence track, another movement, at right angles to it, would go on across the fields. These lemmings did not follow any common track but travelled scattered on more or less parallel courses when passing.

Some animals were seen to come swimming from the south side of the water and, immediately after landing, start climbing up the slope and then continuing over the fields, retaining their direction to the north, while other ones would be coming from the north and, arrived at the shore below the fields, swim over to the south side. However, only on 5 days the weather was calm enough to permit any swimming, while animals coming from the north were observed also on occasions when the wind would exclude all possibility of a crossing. That these animals then deviated from their course and joined the others on the fence track in either direction was observed in some cases, and that all of them actually must have done so can be concluded from the fact that in the intervals between the days when crossings took place, no accumulation of lemmings was noticeable in the vicinity. It is true, that on some occasions and especially at night, a number of newcomers from the north stayed temporarily in the fields to feed, as will be described further on p. 338 but these animals soon disappeared again.

#### *The migration tracks*

It is evident that at many places scent trails from forerunners may play a rôle as stimuli and guidance for lemmings on the move (Myllämäki *et al.* 1962). In the first place the droppings left on paths and migration tracks naturally serve as such. Likewise, when the animals, as described above, were thrusting through dense vegetation or climbing in narrow furrows of the erosion scars, scents might act as sign-posts leading them as on invisible trails. It can also be assumed that scent trails contribute to the initial formation of a migration track. When a flow of lemmings are passing through an area, the first animals choose their route under influence of visual and tactile stimuli from the terrain encountered. The animals coming after them then adjust their course so as to follow exactly the scent trails left by their forerunners, and as the vegetation by and by wears down, a sunken track is formed. It seems that only in this way the narrowness and well defined contours of the tracks can be explained. How mechanically the lemmings follow the course of a migration track, once it is formed, could be seen for instance at the end of the fence track (p 324). Although the new-comers there had the easy grass ground in front of them, they all followed the deviating track that led them down into the close vegetation on the slope. Another example of the same is given further on (p 333).

Up on the sand plateau, where tracks could hardly have been formed in the packed sand and apart from that would have been of no advantage for easy travelling, the lemmings were running on a broad front. On such ground scent trails evidently have no bearing on the animals' choice of course.

Also in the forests within the area, migration tracks formed by the lemmings were met with in many places. Their course was always as straight as the surroundings allowed with only slight deviations in order to use the easiest travelling passages, while keeping the same general direction. In the forest to the west of the sand plateau it was demonstrated that on occasion the course of a track may be maintained without regard to difficult ground met with. The tracks leading west were here found to be going up and down brook banks and crossing several ravines.

Worn down into the moss cover, the tracks in the woods appeared as well defined as the fence track, and where they on occasion would take advantage of a path going in the same direction, their course on this was still visible, as long as the surface was not too hard.

#### *The variation in migration intensity on the fence track*

In an attempt to estimate the variation in the intensity of the migration on the fence track, from the first day onwards counts of the passing lemmings were taken twice daily, in the morning between 9 o'clock and 10 o'clock and at night between 9 o'clock and midnight, always in the same place.

At night a torch was used, which was pointing perpendicularly in the direction of the track and screened off so that no light escaped towards the advancing animals and only a circle of the track and its immediate surroundings was dimly illuminated. This proved to have no disturbing effect on the animals. If, on the other hand, the torch was pointed directly towards them, they would stop running and hesitatingly turn to the side or just sit still.

The counts were taken for a period of one minute and repeated about 5 times, somewhat more, when the frequency was very low. Even in peak nights the animals did not arrive at entirely regular intervals all the time. When for a while a continuous stream had passed, a short period of time could elapse before the next burst of animals appeared. There was always a short wait between each count, starting just when an animal appeared.

A great variation could be noted between the different nights. The figures attained were never less than somewhat more than one to 5 animals per minute but could in peak nights be up to 30–35.

The migration by day was never as strong as that by night. Most of the animals passed in the morning but others could be seen later during the afternoon. The counts in the morning gave figures varying from one animal at intervals of several minutes up to at most 10 animals per minute.

All the figures refer to animals moving to the west. The migration in the opposite direction was not regularly recorded in figures, but a certain check was kept on it. It seemed to be more irregular than the E–W movement. On some nights it was almost absent, on others it could occasionally reach almost the same numbers as the opposite one.

It goes without saying that figures attained during as short periods as these could give only a very rough idea of the intensity. Thus, on nights with a low frequency, the figures would be somewhat too high, since the longer intervals now and then occurring were not included in the time of counting. On the other hand, whereas in the daytime no other lemmings on the move appeared in this part of the fields, apart from those actually passing on the track, on the nights with a high frequency an uncheckable number of animals were on the move both in the stubble behind the observer and on the slope below the track. The true extent of the migration past the place was thus greater on these occasions than the figures from the track would indicate.

The causes of the variations remained obscure. It was difficult to judge if the intensity might be influenced by weather conditions since the prevailing weather, apart from on the days of arrival and departure, was about the same all the time.

Except for two days with a short glimpse of sun and one with sun until noon, there was almost constantly a heavily overcast sky, a temperature of from +2° to +5°C and nearly every day shorter or longer periods of drizzle or rain. Thus, on 9 of the 13 observation nights, the counts were taken in the rain. During the whole period, the wind was either E or W, the latter being against the main stream of migrators.

In the table below are records of the weather conditions during the nights when the greatest numbers of lemmings were moving on the fence track.

Date	Wind	Rain	Sky	Animals/min
27.9	Weak, W	Rain	Heavily overcast	16-20
28.9	Weak, W	Drizzle	Heavily overcast	30-35
1.10	Moderate, E	0	Moon behind clouds, surroundings visible	16-25
2.10	Strong, E	0	Heavily overcast	15-20
3.10	Moderate, E	0	Full moon behind clouds, surroundings visible	25-30
4.10	Fairly strong (direction?)	0	Heavily overcast	23-30

The table shows that high counts were achieved on two nights with rain, viz. 27th and 28th Sept. It could, though, be argued that if rain has an impeding effect on the migration, it is more likely that prevailing conditions, at the time when the animals are prepared to start their nocturnal course, are decisive. Once on the way and under the influence of the migration drive, this might be strong enough to compel them to continue, regardless of a later deterioration of the weather.

The notes from just these two days, however, do not bear out such a view: Sept. 27th: periodical drizzles during the day, from about 19<sup>h</sup> persistent light rain. Sept. 28th: drizzle most part of the day, sometimes heavier showers of rain, in the evening drizzle. Thus, whatever time of the day the lemmings started, it must have been at least drizzling.

On the other hand, on Oct. 7th from 17<sup>h</sup>30<sup>m</sup> there was a dense drizzle, increasing at about 20<sup>h</sup> to a very heavy rain, which kept until 22<sup>h</sup>, whereupon the sky became clear with moonlight. The counts taken shortly after that hour gave figures that, for night-counts, were rather low, 5-8 animals per minute. The fact that this night, due to the moon, was very light, so that the animals were clearly visible even without a torch, could not have had a negative influence on the migration, for on two other nights, when the effect of the moon, though behind clouds, was sufficient to make these nights noticeably lighter than the previous ones, the counts taken were among the highest attained.

After the period of bad weather, the day of departure was as sunny and almost as warm as the first at the place. No recording was made at the fence track, but from about noon the highroad (below p. 333) was kept under observation for some time. The migration there now turned out to be far livelier than on all earlier visits, and even livelier than on the first day.

The observations indicated that a heavy rain in the evening might impede the migration on that night, and that warm sunny weather could stimulate the daytime migration.

As, except on such occasions, no connections between the weather conditions and the variations in intensity could be perceived, it was likely that on the whole the latter were merely accidental, as lemmings arriving at the place were from populations of different origin.

### *The swimming lemmings*

During the few days with calm weather, lemmings were seen crossing the arm of the lake below the fields, which was there about 100 m wide, during the daytime as well as at night. Especially on occasions when the animals were more numerous it could be noticed that they were not swimming straight behind each other but spread on a somewhat broad front, often appearing in swarms of up to a dozen individuals starting more or less at the same time, with the swimmers frequently heading in opposite directions simultaneously.

On the north shore some of the animals started from flat rocks and stones protruding from the shore, which as this point was rocky. Others started from a narrow border of gravel in front of it. On the south side part of the shore was a low sandy beach. The shore-line on both sides of this, on the other hand, consisted of an almost vertical rock, at the time raised about a half to one metre above the water and thus making it impossible for lemmings to climb or descend. All the lemmings starting from the north shore were headed directly towards the sandy stretch, where they after landing ran up the slope and disappeared out of sight. The lemmings on the south side after starting from the same stretch kept to the same route as the meeting ones and almost all landed on the northern shore at the same spots that served as starting points for the latter ones, and from there immediately began climbing up the slope.

A possible explanation for the choice of landing-places could be, that those lemmings that had started from the south shore had, while crossing the water, already at a distance seen the animals moving about on the north shore and that this had induced them to steer their courses straight towards these. The animals coming after them could then simply have followed their predecessors. In the same way, the animals starting from the north shore and seemingly purposefully steering towards the sandy beach, could have adjusted their direction towards the animals coming from there, which saved them from landing at the steep rocks on the sides.

The sight of the lemmings swimming in both directions along a common route would thus be explained as a result of visual influences between the animals.

Also at night lemmings were observed on the north shore, starting and landing at the same places as during the day. Due to the difficulty of keeping the water surface under survey in the dark, the events could not be watched to the same extent, but judging from the number of animals on the shore, the nocturnal crossings were never of the same size as those witnessed in the day.

That lemmings on the move revealed no reluctance to swimming, even when this easily could have been avoided, was demonstrated at some smaller sheets of water in the neighbourhood. Thus, in a small tarn about 100 m wide in the wood, lemmings were seen on several occasions swimming across it, and after landing keeping their direction towards the fields. These crossings were undertaken also at one side of the tarn, where only a short detour would have enabled the animals to proceed on land.

Likewise, once in a nearby peat bog a migrating lemming came running. When arriving at the edge of a small pool it caught sight of the observer in front, and then stopped and groomed. Shortly after, with the observer now hidden, instead of turning a few metres to the side, it went straight on into the water and swam across the 4–5 metres to the opposite side, from where it immediately continued in the same direction.

The same behaviour was observed, too, on not so few occasions, at small lake inlets in this and another district.

*The migration at a highroad*

From the day of arrival and every time the place was visited, a migration of lemmings was noticed at the road which, after rounding the north end of Kallsjön, runs southwest passing Sundet.

For the first 3 km it goes more or less parallel to the lake and, except in some places, is high above the water, on the wood-clad slopes of a hilly area on its north side. For some stretches it skirts the lake, so that the whole space between the road and the water below is covered by its supporting construction of big stone blocks, forming a steep descent down to the shore line, while along other stretches a belt of forested ground of varying width separates the road from the water.

Most of the lemmings came walking along the north side of the road in the draining ditch, which here was not more than a shallow groove between the road and the sandy or rocky slope above. Frequently, however, animals would at the same time come trotting on the tarmac of the roadway itself. From this level the lake was visible below the steep slope, but for the animals walking in the groove, the view was screened off by the road. They would come one by one with the distance between them varying from some 5 metres to more than a hundred, depending on the intensity. Occasionally an animal walking on the road was seen to approach the lake side and at last disappear into the vegetation there, but these deviations were observed only on stretches where the ground outside was on a level with the road. No animal was seen climbing down the stone-covered stretches.

Most of the animals were heading eastwards but some were also bound in the opposite direction. These proportions varied somewhat on different days.

In two places, where parts of the rocky hillside on the north side of the road had been blasted away, the remaining rocks now formed a high perpendicular wall along the roadside. Below these rocks lay scores of lemming carcasses in different stages of putrefaction. They were the remnants of lemmings that had come down from the slope above and fallen over the edge of the rock. Every time these places were visited, there were new bodies added to the previous ones and on some occasions the observer actually witnessed how lemmings even in daylight would become victims of these death traps, evidently due to the presence of tracks on the slope above, leading down to the edge of the rock.

Here and there on the road lay the scattered bodies of other lemmings killed by passing cars. Migrants arriving at these bodies were frequently seen to stop and eat the exposed entrails, not infrequently with the result that they in their turn immediately after were run over and became a fresh supply of food for their successors.

*The general direction of the migration through the area*

It was obvious that not all the lemmings appearing in the continuous stream on the fence track, as well as those seen passing the district at other spots, and in addition all those that had passed there during the weeks or months before, could have originated in the comparatively narrow belt of fell areas situated on the Swedish side of the border. They must have to a large extent involved animals from far off breeding grounds in Norwegian fell districts.

From observations it could be concluded that almost all the lemmings wandering on roads, paths and tracks within the area between the north end of Lake Kallsjön and Sundet had come down there from the north, that is by maintaining a more or less southern direction. A small scale migration in the opposite direction was represented by the lemmings seen crossing the lake

arm at Sundet from the south side and continuing across the fields. Their further course was not traced.

Of the animals from the north, those that reached the highroad where this runs along the lake, turned aside and followed it either to the east or to the west.

The lemmings going westwards remained on the road only as far as it is in contact with the lake. Where at the west end of the lake the road continues to the west, the animals deviated to the south into a forested peninsula beginning there. The stretch of the road between the lake end and Sundet can be regarded as the base of the latter. Along this stretch (as well as further to the west) there was no migration on the road in either direction, but animals arriving at it from the north crossed it and contributed to the flow entering the peninsula. Arriving at the south end of this, the animals deviated to the west and, proceeding on paths, migration tracks and a cart road, then appeared at Sundet as the stream passing on the fence track. Other animals would arrive at the fields directly from the north.

Beyond Sundet, the steeper shores of the arm of the lake and further on the rapid stream from Lake Anjan would prevent the lemmings from crossing the water before reaching the east end of the latter lake. Considering that they had previously deviated to the west due to the blocking effect of Källsjön, it could have been expected that when arriving at Sundet they would attempt to resume their earlier direction, as there they had the best opportunity of crossing the water. On the contrary, the animals on the fence track, as described above, showed a marked disinclination to any contact with the shore-line, while other lemmings simultaneously on the move crosswise to them did not hesitate before a crossing whenever the weather permitted.

The original direction of the lemmings running on the fence track in the opposite direction was never traced. After passing Sundet to the east and entering the peninsula they proceeded along its eastern side and, as some observations indicated, came up to the road and joined the eastward migration on it.

The further course of the lemmings wandering on the highroad towards east could never be ascertained by direct observation. They all disappeared by degrees into the woods on both sides of the road before this reaches the very end of Lake Källsjön. On several occasions the roads leading from there further to the east were patrolled. Here and there lemmings on the move would be seen on and around these roads, but at the time rather sparsely and most of them were heading in the opposite direction to the west towards the lake end. A short and rapid stream emerges there, forming the outlet of the adjacent lake above. It effectively prevented the lemmings heading east from rounding the lake and deviating to the south. Their only possibility was to swim across either of the lake ends above or below the stream, or to use the bridge across this. According to a report, earlier, in August, a great accumulation of lemmings had been observed here at the north side of the stream and the animals had then been seen to continue to the south, using all the possibilities mentioned.

It is of interest that at just this spot lemmings on the move in the opposite direction were seen in the following spring (p. 355).

During the observer's visits to the place only stationary lemmings were found in the vicinity. In calm weather, however, single lemmings would now and then be seen swimming to and fro between small islets near the end of Källsjön, as well as between protruding points along the shore of the lake above. Although this did not indicate any uniform direction but rather suggested tentative movements, it can be assumed that the animals arriving at the place sooner or later crossed either lake end to the south. Other experiences suggested that this took place at night and thus was overlooked.

*Discussion*

The counts at the fence track showed that during the observation period there was no general decrease in the migration intensity. In spite of the high records now and then attained, there were, however, some indications of a peak having occurred earlier within the area. According to reports, there had earlier at three places been concentrations of lemmings of which at the time nothing was found. Likewise, within the woods there were at several places localized migration tracks that at the time looked entirely abandoned. They were, however, only inspected in daytime so this impression might have been wrong, but it may well have been that populations of migrants that had previously passed through the area had used them, while the present ones did not.

When comparing the present observations with the experiences recently made during an autumn migration at the lake Kilpisjärvi in the NW corner of Finland (Myllymäki *et al.*, 1962), one may note similarities as well as some distinct divergences in the behaviour of the lemmings studied.

While the migration at Sundet during the whole observation period was, though to a lesser extent, going on also in the daytime, the migration at Kilpisjärvi turned out to be entirely nocturnal. It was also less intense at the place chosen for recording and never attained even the lowest counts noted during the nights at the fence track.

Migration on paths, noticed also by earlier authors, is mentioned by Myllymäki *et al.* and these authors found, too, among the "wandering trails" one made by the lemmings, thus the same kind for which the term migration track is used in the present paper.

Myllymäki (op. cit., p. 6), however, emphasizes as typical some patterns of the migration routes chosen which were hardly ever noticed at Sundet, viz. "a 'visual bank' offering shelter on at least one side (danger shadow)" implying that the lemmings on the move avoided running along a trail without such protection that could be offered, for instance by "shrubs, tall grasses and rocks" along a path, or by the slopes of a ditch.

Contrary to this, the observations of the migrants at Sundet bore out clear evidence that any protective features along their routes were inessential, even where the routes could easily have been chosen so as to offer such protection.

Thus, as mentioned, the fence track was at a distance of about 1 m from the fence all the way, where its formation had been easiest to achieve, instead of close to it, where the vegetation would have screened the track on one side. Likewise, the animals up on the naked sand plateau unhesitatingly would run anywhere along its centre and none was seen keeping close to its border along the descent, where the original ground surface was left and where its vegetation in parts formed a low bank just as described by the authors cited.

Above (p. 333) is mentioned that lemmings wandering on the highway were using the shallow draining groove between the steep slope above and the roadway. Due to this slope on one side it undeniably fulfilled the requirements for a migration route as described by Myllymäki, but it was also in fact the only one with such characteristics met with during the observations. At least those lemmings that were at the same time frequently seen trotting along on the tarmac roadway itself, with the bare rock sloping down to the water at the other side, and thus visible from a far distance, revealed by their behaviour that they felt no urgent need of protective surroundings and that in this case the preference for easy ground on which to travel was preponderate for their choice of route.

Contrary to this, Myllymäki from observations at a highway was led to state that although "lemmings were ascertained crossing the highway transversally", "no lemming was ever seen running along the highway" and that "the highway probably exceeds the 'maximal breadth' character belonging to the wandering trail, i.e. the 'bank' formed by shrubs (or forest) is too far away to correspond to the visual character of a protected side".

The discrepancies found in the behaviour of the migrants at Sundet and at Kilpisjärvi might be accounted for by the local circumstances. At Sundet the bulk of the migrants had most likely come from far away and had consequently already for some time been on migration. Kilpisjärvi on the other hand is situated in the sub-arctic region, and at least a part of the lemmings on the move there might have originated in the surrounding district, the migration thus being at its onset. Migration by night alone, when it usually is found to be at its strongest, and the earlier time for the observations could also be indications of an earlier stage of migration, during which the wandering animals were still retaining some of the more wary behaviour pattern pertaining to lemmings in their normal haunts.

Though it is likely that the formation of migration tracks made by the lemmings is typical for all migration years, their existence seems to have been overlooked by almost all observers on lemmings. As early as in 1740 runs of this kind are described by Linnaeus. Probably only supporting on him, Zetterberg (1833) mentions them, but later they are not again referred to in literature until by Myllymäki.

The use of migration tracks by the lemmings gives an indication of how great masses of migrants may be passing through a wooded country rather imperceptibly, as long as they do not meet with some obstacle which results in the well known accumulations. It remains, though, to discover how far away from the fell districts that such tracks may still be formed. During the present studies they were found further away from the fell districts within a peninsula in Lake Storsjön (p. 345), but it is to be expected that the farther the migrants spread out into the lowlands, the less the chances become for the formation of such tracks.

The sight of the lemmings on a migration track, appearing in full daylight across an open field, heading on without any trace of their usual vigilance, gave a strong impression of the difference from the stealthy way of moving otherwise typical for small rodents. Considering the distances that lemmings are able to cover in a migration year, it is clear that such a task would be impossible to achieve within a reasonable time without an adjustment of such traits of behaviour that would hamper rapid movement. The absence of their normal shyness, typical for lemmings on migration, becomes, thus, a time- and energy-saving factor. For the same reason the mechanical running on tracks is also advantageous, and once formed the tracks relieve the succeeding migrants from continually making decisions as to which route to take. However, this reliance on the tracks occasionally can be fatal for the animals, as was demonstrated at the highroad (p. 333).

Whereas migration tracks with their scent trails may have a stimulating effect on the migrants, it was obvious, on the other hand, that no difference in the way of moving could be noticed at places where the lemmings came running without any track to follow. When heading on, for example, across the sand plateau or on a road, their movements appeared equally unhesitating and purposeful, whether other lemmings were within sight in front of them or not.

Collett (1911–12, p. 152) is of the view that the migration drive is released by the

sight of other lemmings on the move, and if an animal on migration is taken away from its fellows and isolated, it thereby loses the drive to migrate.

Whatever stimuli might be at work at the onset of migration, it was obvious that such influences as Collett vindicates could not be valid for the animals seen here. All the present observations of single lemmings passing on roads, paths or migration tracks, with long intervals, before the next one appeared, as was the rule in the daytime, demonstrated adequately that each individual was carrying out its wandering entirely independently of other migrants. That this is the normal way for lemmings to move during migration cannot be doubted.

The migrations studied by Koponen *et al.* (1961) in the spring and by Myllymäki in the autumn showed the same pattern with singly moving animals.

Though, when the lemmings at Sundet were crossing a water, the situation was different. When appearing in flocks their behaviour suggested a mutual influence between the swimmers at the start and during their crossing.

That lemmings on a shore may hesitate and then start in waves is pointed out also by Myllymäki (op. cit., p. 10 ff.), but whereas these authors conclude (p. 11) that "water generally seems to be a rather strange and unattractive environment to lemming" this statement should probably be restricted to hold good only for broader sheets of water. While the above related behaviour of the migrants at the spruce brushes (p. 326, 328) was suggested to be due to a strong reaction to a water front, the incidents observed at other sheets of water (p. 332) are on the other hand more in accordance with the experiences of Collett who states (op. cit., p. 151) that the animals are partial to moist places and cross any pool, even if it could be avoided by a few steps.

#### *Notes on the behaviour of the migrants*

##### *The way of moving*

The lemmings seen wandering on the fence track as well as those using paths, roads and similar even ground moved at a typical even-paced trot, which at a glance distinguished the migrants from other animals just occasionally moving from one place to another. A change from the regular pace could on the other hand be observed under certain circumstances. Thus, if an animal for some reason left the fence track and continued in the stubble at the side, its trot would be exchanged for a hopping gait in order to proceed more quickly on the uneven ground. Sometimes the animals, while still trotting, would increase their speed considerably, as was the rule when they were running on the sand plateau. It could then clearly be seen how lemmings on the move keep their bodies well raised on high legs.

##### *The behaviour of the migrants towards each other*

On those nights when the migration on the fence track showed a peak, the movements of the animals were not so regular as when they came more singly with longer distances between them.

Turning up perhaps 3 to 6 at a time, one hard on the heels of the previous one with an interspace before the next small pack appeared, they seemed to be in more of a hurry than under other circumstances. Sometimes an animal coming from behind made a rush and tried to run past the one in front. As all of them endeavoured to keep to the narrow track, this inevitably gave rise to shoves in passing, requited by annoyed squeaks from the animal pushed aside. Such incidents, however, never caused any further reactions between the animals involved, which without delay

headed along as before. If two animals coming from opposite directions suddenly met on the track, a short squeak would sometimes be heard as they stopped for an instant nose to nose. Then one darted aside whereupon both rushed on in their original directions.

Although there were thus never any pronounced signs of hostile relations between the migrants, on peak nights a certain irritation was noticeable between them. Walking along the track one could then hear everywhere more or less subdued squeaks evidently caused by the animals jostling one another when thrusting forwards through the dense vegetation on the slope between the track and the shore below.

#### *The reactions of the migrants to danger*

The lemmings on the move never paid more attention to an immobile observer than to other objects encountered along their route.

If thus the observer was standing directly on the fence track they came running straight on, both by day and by night, without the slightest hesitation, just passing between or swerving past the rubber boots within some cm, occasionally giving them a sniff in skirting them.

They would easily react, however, to a sudden movement and then generally rapidly turn to the side and take cover in the long grass on the edge of the descent. Sometimes, though, instead of this they swiftly turned round on their heels and ran back along the track up to 5 or 6 m before turning aside and hiding. This reaction which obviously would have been disastrous in the presence of a real enemy, was evidently due to a tendency in foreign surroundings to adhere when possible to an already explored route when avoiding a sudden danger. Another incident showing this will be related further on (p. 354).

One day, in order to catch some lemmings for examination, the observer kneeled at the side of the fence track with one hand held ready about half a metre above the run. In spite of this short distance it happened not infrequently that the passing animal dodged aside in a flash just as the hand went down, so that the clutch missed. Several times it then occurred that instead of rushing into the grass, the animal quickly ran and hid between the knees or boots. The tall immobile object nearby was thus not associated with the menace from the moving hand.

In order to find out at what distance lemmings on the move in daylight would react on seeing a danger, the observer once placed himself upright on the highroad in front of the animals heading along the middle of the roadway. When waving the arms up and down it was found that the approaching animals reacted by rushing aside at distances of 15–16 m. When instead posted at several different distances at the side of the roadway and then starting waving just as they were passing on this, their reaction would appear at about 30 m, due to their sight being more adjusted to a lateral field of view.

#### *The temporarily resting migrants*

Besides the lemmings actually seen wandering past the place, scattered occasional visitors were always found feeding in the fields. Their numbers varied in proportion to the migration simultaneously going on. On those nights when the counts at the fence track revealed a greater movement than on the preceding night, this relation became clearly noticeable, especially in the field above it.

Whereas earlier during the day, at the most, a few such visitors might be observed here, in some parts of the field there could now be found up to one animal per square metre. By this, as

well by their behaviour, it could be concluded that these visitors were newly arrived migrants making a temporary rest. The observations indicated that a part of them would arrive by the fence track and while feeding turn on to the field, while the remainder had come down there by a movement directly from the north. By the next morning their number had dwindled, though a minor part would be still staying on, and single individuals might do so for another night. This could, at least, be stated in one case when ten animals were caught and marked by a clip in the pelt. One of these was recovered during the following night.

### *The reactions of the resting migrants to danger*

When the fields were patrolled during nights with a high migration intensity, the numerous lemmings then resting and feeding there showed a behaviour that turned out to be clearly different from that of the stationary lemmings (below p 340). When approached and having no places in which to hide they frequently made front to the observer and assumed their well known threat posture with their heads raised and mouths open while emitting squeaks and growls sometimes accompanied by jumps into the air. Others after a squeak would rush away from the vicinity. When the observer slowly walked along, the same angry squeaking and growling would be heard from all sides in the dark, outside the circle of light from the torch, thus not only from the animals directly confronted in passing. It seemed that the latter animals, by their squeaks and rushes, caused a general excitement among other individuals within hearing, which gave rise to the same reaction.

*A different reaction to danger: the crouching posture.* Among the lemmings in the fields there were some individuals that showed a different reaction to the approaching observer. After running a few metres they would sink down and crouch, their behaviour bearing a striking resemblance to that of young waders under similar circumstances. Lying with their heads directed forwards and the chin against the ground, they would remain so no matter how near they were approached.

A slight touch of the boot would make them rise and run forwards, usually only to resume the same posture after a few metres. When walking around the fields, such crouching lemmings could be found also where no running animal had just before been observed. From this it appeared that some of the feeding animals, when aware of a danger that did not appear to them as all too imminent, would react to it merely by sinking down and crouching on the spot instead of first running away. It could not be made out whether they behaved so in response to squeaks from other lemmings or to the sight of the observer.

It was somewhat unexpected to find that also in the daytime lemmings could be seen in the crouching position. Lying on the short stubble and thus visible from far off, these, too, allowed themselves to be approached as close as during the night.

One night when some lemmings in the crouching posture were pushed away, two of them ran straight away to the border of the field and disappeared into a shelter, by that showing that they belonged to the gregarious animals housing there (below p. 340), but all other observations of the crouching animals indicated that they were temporarily resting migrants.

It may also be noted that this crouching posture obviously was not the same as the posture that can sometimes be observed in other small rodents when frightened for instance by a sudden noise. In such a case the animal may become immobilized in the position it happened to have at the moment, e.g. sitting with one paw lifted etc. The author has in the field noticed such a "freezing" in both the bank vole (*Clethrionomys glareolus*) and field mouse (*Apodemus* sp.).

*The stationary lemmings*

*The stationary lemmings in the fields*

Of the stationary lemmings, those living in the open fields were for obvious reasons easiest to observe. Within the area the greatest number of them was, at the time, to be found in the fields of Sundet.

In some fields situated on the outskirts of the cultivated area and adjoining forest ground, stationary lemmings occupied with feeding would in the daytime be found scattered over the area. In some places they would appear more numerous than in others, but what could then sometimes look like a loose grouping was only due to some parts of the area being more attractive than others for grazing. Dwelling out there in the open fields these animals were visible from far away. In spite of having no shelters within reach, they appeared, however, entirely unconcerned about the surroundings and were never seen to interrupt their occupation to keep an outlook for possible dangers. When, though, the observer entered such a field with grazing animals, they all unhesitatingly went running the shortest way to the next border and disappeared, scattering among herbs and shrubs. All of them were obviously well acquainted with the place and none stopped to assume a threat posture.

Besides such animals, two special categories of stationary lemmings could be distinguished, the gregarious and the resident lemmings.

*The gregarious lemmings.* These animals had adopted a kind of sociability and appeared as groups counting from half a dozen to about a score of individuals, each group with a common hiding-place to retreat to for rest and shelter. They were of the same size as the above mentioned stationary ones, i.e. not full-grown animals of the year and, judging from samples taken (p. 343), sexually immature. They were found in places situated at some distance from such field borders that adjoined ground with a natural vegetation. Their hiding-places could be situated for instance between the roots of a willow bush, under a pile of boards or hurdle poles or other similar objects present at the borders of a field. The members of a group were found staying day after day at such a place during the whole observation period. When feeding out in the field and disturbed by a passer-by, they went dashing from all sides towards one and the same place, purposefully making for their special shelter.

The term gregarious used here for such animals is, however, only meant to denote their adaptation to sharing a common refuge. When feeding out in the fields they behaved independently of each other in the same way as all the other stationary lemmings.

*The causes of sociability in the gregarious lemmings.* Contrary to the other stationary lemmings, the gregarious ones were found only in the fields, and their adaptation to a kind of social life was clearly dictated by their preference for certain characteristics of the vegetation on their feeding ground and the necessity of having a shelter within reach of it. As the areas attractive to the animals did very seldom border on forest or other unfarmed ground, there were generally no natural hiding-places available there. The lemmings in such areas had then taken to artificial shelters as exemplified above, and as these places were rather few and far between, this had induced the animals to congregate around them.

As in other farms in that part of the province, the fields at Sundet were used only for growing green forage. Each field is left a number of years before it is ploughed and resown. As all the fields are not ploughed the same year, there were considerable differences in the state of their vegetation as to the species of grasses and herbs dominating in them at the time. It was this factor that

determined the abundance of the different categories of lemmings. The areas preferred by the stationary lemmings were either the older fields in culture, all at the time harvested, or still older ones, left unploughed for many years and only used for grazing cattle. The vegetation in the latter consisted in parts of tussocky grasses which at the time were looking almost entirely withered.

It became evident that the youngest fields were not frequented by animals familiar with the surroundings. So for instance the field next to the fence track was the most recently ploughed one on the farm. Temporarily resting migrants were, as mentioned (p. 338), often seen feeding in the stubble of this as well as the other fields, on some nights in great numbers, but hardly ever any stationary lemming was seen here. This was not due to any lack of hiding-place nearby. At one end of the field a stack of planks provided shelter for a group of gregarious animals. These, however, preferred feeding on an adjacent old grass area, originally kept as a lawn, but since left to itself and at the time looking brown and grazed down, appearing only to offer a very meagre pasture.

*The resident lemmings.* The resident lemmings were animals that had settled down as solitary dwellers, each in a burrow surrounded by a runway system. They were noticeably bigger than the rest of the stationary lemmings and, by appearance, all adults.

A number of such animals had their dwelling-places in the middle of a field which had been harvested earlier in the season. At the time most of the hurdle-racks had been removed and the holes from the hurdle-poles were now taken in possession by the animals for their burrows. From each of these holes a system of winding runways, some at a length of up to about 20 m, radiated out in all directions, sometimes in contact with the next system. The runways had obviously come about not merely by frequent running but by digging and gnawing so that they were now sunk into the surface of the soil. In one of the runways, at a distance of some dm to a metre from the hole in the centre, there was always a heap of droppings. It could not be proved, but seemed probable that each burrow was housing only one animal. A lemming would often sit outside its hole, while others were feeding in the field around. Although it was observed on some occasions how, when scared, several animals at a time, by using the runways, disappeared headlong into the same hole as the lemming sitting next to it, this should probably rather be interpreted as an emergency in an urgent case.

Other residents were found in an adjoining old field overgrown with numerous tussocks of long grass, scattered juniper and willow saplings. Here the burrows were dug out into the sides of big tussocks of moss (*Polytrichum*). Runways, with heaps of droppings outside the holes, were also present here, but the run systems were by no means as extensive as in the other field mentioned. In this field, there was apparently not the same necessity for precautions facilitating a quick escape from longer distances into a certain burrow, as there were opportunities for finding an occasional shelter anywhere.

None of the immature lemmings in the fields was found to have settled down in a burrow of its own, though it was observed, both day and night, how such animals when feeding around empty hurdle-pole holes, would occasionally run and hide in them when scared.

#### *The stationary lemmings in the woods*

Stationary lemmings were also to be found in the woods of the district, but due to the difficulty of surveying that kind of country it was not possible to judge to what extent the animals had chosen to settle down in such habitats.

In the woods, here mainly composed of conifers, the lemmings seemed to avoid the most densely wooded areas as well as those with ground cover of the extensively growing bilberry (*Vaccinium myrtillus*), which was never seen accepted as food.

Immature stationary animals were encountered mostly in small peat bogs with sedge (*Carex*) and mosses. At these places they would be seen scattered while feeding in the open. They behaved as the non-gregarious lemmings in the fields and when approached would rush away in various directions towards the borders of the open area and disappear in the surrounding vegetation.

The presence of resident animals was also revealed, in small glades in the wood with a cover of mosses and grasses and where a stub or a windfall could provide a shelter. Short runways led to their holes under these, always with a heap of droppings present in the vicinity of the hole. These residents seemed to lead a more secluded life than those observed in the fields, at least the inhabitants of the burrows were rarely seen outside.

#### *Notes on the behaviour of the stationary lemmings*

##### *The gregarious lemmings*

From all daily observations of the gregarious lemmings it became evident that they were living together in the greatest amity and in no way showed any reluctance to being crowded. Thus, on several occasions, when a disturbed group had disappeared under a pile of poles or planks and after a while still no sound was heard from them, the hiding-places could be uncovered, and up to 15 individuals found, sitting packed together in a narrow space.

It may be stated that during the whole observation period the stationary lemmings were seen in activity at many times of the day. When the gregarious lemmings, were not feeding out in the fields away from their shelter, they would frequently be found outside it, moving around or just sitting. There is no doubt that they periodically withdrew during the day, but although some groups were visited daily, no watches consistent enough for recording the intervals were kept. Just at dusk, however, the number of them always decreased, and later in the night the same places would look entirely deserted or with just a few animals visible.

By pacing up and down along the middle of the fields around and clapping one's hands, it was then possible to make out the different categories of lemmings feeding there at the time. Most of the animals rushed away in all directions, though not up to the borders, while some others made front and showed the threat posture. All these were obviously casual visitors in the field. However, now and then a few others were found among them which were seen running purposefully straight to their hiding-places at the borders of the field.

It was thus evident that with a few exceptions the gregarious lemmings used to remain inside their shelters in the night. This statement is made with the reservation that the fields never were visited after midnight, and consequently it was never checked whether the animals appeared again in the darkness of the small hours.

In the neighbourhood of their shelters the gregarious animals showed but little fear of a human visitor.

One group had quarters on and under a dilapidated old wooden bridge over a ditch, with their feeding grounds in the fields on both sides. A number of them would always be found moving about or sitting on the bridge and, during the short spells of good weather, basking in the sun-

shine. If the place was approached they all ran and hid under the logs and boards but very soon came out again, resuming their activities without being in the least disturbed by the observer sitting near by. Thus they could conveniently be filmed at a distance of about a metre.

### *The resident lemmings*

As far as was ascertained by the observations of the resident lemmings, these, too, lived in peace with other lemmings in their neighbourhood. Thus, an animal sitting outside its hole was never seen to object to other lemmings passing nearby.

How far this indulgence stretched when it came to actual visits in the burrow, was more questionable. Twice it was witnessed how, when scared by the observer, three or four animals rescued themselves into one and the same hole. When the first excitement was over, some squeaks were heard and the ones sitting nearest the entrance flew out one after the other, obviously ejected by forcible pressure on the side of the holder of the burrow. But in another case no such incident occurred, all remaining quiet until the animals reappeared.

The resident lemmings were somewhat more wary than the gregarious animals and if approached while feeding out in the field quickly dashed into the nearest runway and by following its winding course rapidly reached the hole. When the observer then sat down motionless there was, however, never any long delay before a head appeared in the hole, and soon the animal was sitting outside and could be watched from a distance of a few metres.

### *The size and reproductive status of the lemmings around Sundet*

In order to obtain some information of the size and the reproductive status of the lemmings, some small samples were taken at various places around the farm and in the woods.

Most of the lemmings passing on the fence track were rather small specimens. In the morning of Oct. 6th, a sample was taken there by catching the animals as they came running past, weighing them and then letting them down again, except for a few that were killed and their sex determined. All were taken without bias as to their size, a new lemming grasped as soon as the recording of the previous one was ready.

Of the 21 specimens thus examined, 17 weighed between 30 and 47 g (mean 38.7). The dissected females had a juvenile uterus, in the males the testes were about 3 mm in length. Between these immature specimens there came now and then also adult animals on the track and of those caught, two were females weighing 59 and 68 g and two males of 88 and 91 g.

During the stay in the district another 30 lemmings were caught, killed and dissected.

Of these, 8 were taken among the stationary lemmings (not resident ones) and weighed between 37 and 44 g. They all had a juvenile uterus or testes (3 mm). Judging by sight, the bulk of the stationary lemmings as opposed to the resident animals, were of about the same size as these.—It should be noted that lemmings of this size cannot by size alone invariably be denoted as immature. In July of the lemming year 1960 the author was collecting specimens in Lapland in a fell area where both wandering and stationary lemmings were encountered. Among the pregnant lemming females caught there the smallest ones weighed 27, 28, 32 and 43 g respectively. In five males weighing 46–48 g the testes measured from 9 to 10.5 in length.—Of the samples taken at Sundet, the remaining 22 specimens were purposely picked out among the lemmings encountered because of their bigger size. Of these, 4 ♀♀ (65–72 g) and 5 ♂♂ (77–91 g) were wandering animals and 5 ♀♀ (70–97 g) and 8 ♂♂ (80–106 g) resident ones from the fields. In one ♀ resident the uterus was enlarged with visible blood vessels though not yet with discernible embryos, in the remaining

8 ♀♀ it was regressed with placental scars. In one ♂ the testes were noted as "small", in the other 12 they measured from  $5 \times 7$  to  $8.5 \times 13$  mm.

The above figures indicate that in some males the testes were in an active state, in others not. Any difference in this between wandering and stationary specimens could not be proved. Three ♂♂ taken among the resident animals contained a rich supply of subcutaneous and interintestine fat.

During the whole time 4 small young ones, from appearance aged between 2 and 3 weeks, were found between Sept. 27th and Oct. 1st in an old field where resident lemmings had their burrows. These young ones and the pregnant ♀ mentioned above were the only proofs of breeding that were noticed at the place during the observation period.

### *Discussion*

The general behaviour of the immature stationary lemmings showed that such animals do not feel any urge to disperse from each other's neighbourhood, and the aggregations found among a part of them demonstrated that lemmings, when induced by the local circumstances, may evince a social behaviour beyond merely tolerating other individuals in their vicinity. As such a sociability prevents any competition between the animals in regard to necessary shelters, it renders possible a full use of the most attractive feeding areas.

It is natural that in distinguishing between the different categories of lemmings, cases came up that appeared more or less transitional.

Where gregarious lemmings were found as holders of natural hiding-places, and one of these consisted of a willow bush standing isolated at a field border with the animals moving around it, this gave a more spontaneous impression of a defined colony than when their quarters were spread along an old ditch overgrown with tussocky grass, with holes and galleries behind as shelters. Still, these places, too, were in constant use, whereas other stationary animals scattered in the fields and peat bogs, seemed to run and hide in the vegetation at the borders without regard to any fixed places.

On the other hand, the temporarily resting migrants were not, in some cases, clearly distinguishable from the latter category. Occasionally it was observed how the latter ones, too, when encountered while feeding at places with holes in tussocks available close by, would silently run and hide in these.

The question may also be raised whether, during the whole time, it was the same individuals that appeared as stationary, or if any of them after some time resumed their wandering, and further if among the newly arrived migrants there were any that not only made a temporary rest but stayed on for a longer time, in cases making up for other stationary ones that might have gone. Such new-comers mingling with stationary animals would rapidly learn to know the surroundings and so become indistinguishable from the others.

The quarters of the resident lemmings were obviously similar to those used in their natural haunts, and it could hardly be doubted that these animals had settled down definitely at their burrows and runways and "intended" to meet the winter there.

As for the immature lemmings such an assumption would be more precarious. Although the gregarious animals at the time appeared to be stable groups, this

could not be confirmed by direct observations, and the rest of the stationary animals were obviously still less possible to control.

Collett (1911–12, p. 152) mentions that during their wandering in the lowlands lemmings may stay at a place for weeks and months but then suddenly disappear.

#### Some observations and reports from other districts

##### *Observations on a mass concentration of lemmings*

In the autumn the peninsula of Hammarnäset in Lake Storsjön had for a long time been the scene of an exceptionally large scale invasion of lemmings, which was brought to notice by the local people and attracted the attention of the press. The author made two short trips to the place, and as the behaviour of these migrants revealed some unexpected traits, an account of the observations will be given.

On Oct. 23rd when driving down along the peninsula, in a daylight turning into dusk, scattered run-over lemmings were passed, at places more numerous; a few living ones were also seen. Returning some hours later in the dark, it became evident that many animals now were on the move, specially along the kilometres next to the south end. Now they were encountered in groups on the road, running to and fro in the light from the car. As there was no time to stop, it could not be decided whether the animals when undisturbed were moving towards the south, but judging from later experiences this was most probable.

The next morning flocks of feeding lemmings were seen in some fields situated about 12 km from the south end of the peninsula and in others, not far from the end, hundreds of such stationary lemmings could be seen at a time. Animals on the move on migration tracks were also observed. Arrived at the south end only a few were seen at the very shore but on the vast surface of the lake, now like a mirror, many hundreds of lemmings were floating, drowned during an unsuccessful attempt to cross the lake. The days before there had been a wind.

On the second trip to the district on Oct. 29th, there were stationary lemmings in the fields next to the south end, taking shelter under piles of stakes or hiding at the border of the adjoining wood.

This wood, mainly composed of conifers, was stretching as a long belt between the fields and the stony shore line. Inside the wood hardly any lemming could be detected, but that it had been used extensively as a feeding-place for masses of them was clearly proved by the fact that literally all available mosses and herbs were grazed to the extent that the ground in places now was denuded of all vegetation.

In the following night the place was visited again. Now lemmings were on the move along the border of the fields. About 21<sup>h</sup> the observer walked up to the southernmost point of the shoreline, where the open strip of shore, covered by rubble-stones and gravel, became broader. Here it projected into a point, which continued as a low spit, directed straight out into the lake for about 85 m, from its broad base narrowing to averagely 1–1.5 m across. During two previous visits, only a few lemmings had been found on the shore and none out on the spit.

When now coming out of the wood, the scenery had totally changed. The whole shore around the point, as well as the spit, as far out as the torchlight could penetrate the prevailing heavy mist, was literally covered by a compact mass of lemmings, while the air was filled by a kind of unison, high-pitched but soft, twinkling noise that had already been heard from far away. It did not resemble anything the observer had previously heard from lemmings but reminded rather spontaneously of the call-notes from flocks of small waders (*Calidris alpina* and *ferruginea*) at their feeding-places during migration. When the light was wandering over the nearly immobile masses, there arose some movement among the animals within the light-circle, like waves rolling

from one side to the other, and when approached, the crowd around floated aside like a living carpet. There was never any disordered rushing among the animals which were moving uniformly, head by head and turning synchronously in one direction or the other with a striking precision.

Assuming that the accumulation had in spite of all not yet attained its peak and that more animals might still be on the way down to the place, the observer's intention was to return some hours later. Noticing that his presence (and/or the torch-light) caused a certain anxiety among the animals and not wanting to hinder in any way possible newcomers from joining them, he therefore withdrew.

Coming back about midnight it became clear, however, that the assumption about the time for the peak had been erroneous. Though the sight was still impressive, the masses had noticeably diminished when we, now three persons, walked out to the spit. There, some groups of animals were still holding their places. On our approach the flock next to us came running towards us and turned aside at the base of the point. But once we were out on the spit and standing there all three across it, thus blocking the passage, one swarm after the other came out again from the shore towards us. After some hesitation the animals began searching their way to the best of their ability between our boots in their eager efforts to proceed further out. Meanwhile, some other undisturbed animals were seen to go into the water and start swimming along the borders of the spit. Single ones among them would occasionally head away from it, but after having made a circle they all came ashore again on it and there was no indication of any lemming actually leaving the spit for good.

This spectacular nocturnal accumulation of lemmings was not, which could have been expected, only an occasional phenomenon. Lemmings had, it was reported, been observed in the northern part of the peninsula already at the beginning of September and in the following time in increasing numbers appeared in the fields towards the south. At what time this had given rise to the great concentrations at the point could not be established, but at any rate it had already been observed for some weeks before this visit.

The course of events as reported by people from the district had previously been the same as now, the animals coming down to the shore at night and then withdrawing again before dawn, leaving the spot deserted during daytime. An account from the same place some week earlier has recently been published by de Kock and Robinson (1966). At that occasion, too, the same return movement was witnessed.

An invasion of lemmings into the peninsula was by itself nothing remarkable considering the topographical circumstances. For animals coming from the north and wandering in a more or less southern direction, the water system referred to (p. 3<sup>22</sup> and further on p. 348) would act as a catching arm leading them into the funnel formed by the peninsula.

For lemmings arriving at the south point, the vast water surface with the opposite low land contour hardly visible even in daylight must appear deterrent and make them hesitate to proceed across the lake. Besides, a prevailing wind would be sufficient to restrain them from this.

The distances the swimmers from the point would have to cover before reaching land varied according to which direction was chosen.

If heading to the S or SW, they would attain the mainland about 3 km away at the west shore of the lake. Available reports stated, though, that no lemmings had been visible on that side. If choosing the direction straight to the east, which was the least probable, this would imply crossing the lake at its broadest, about 15 km away. By continuing instead in the same direction as the axis of the peninsula itself, i.e. SE, they would after swimming 3.5 km meet with the first of some small islets that could be used for a temporary rest. Further away there lay other bigger islands along their course so they would never have to swim more than two km at a time.

passing from one island to the other and thus attaining the mainland. In fact, circumstances at the east side of the lake indicated (p. 348) that this was actually the direction taken by the animals.

These distances are not longer than others reported for swimming lemmings. Thus Collett (1911–12, p. 151) mentions lemmings crossing a lake 4 km wide, and on another occasion swimming in the sea from one island to another 5 km away. It seems, however, that in both these cases the country in front of them was elevated, and as the same author elsewhere (1895, p. 49) remarks, "it would seem as if no stretch of water were too wide for them to cross if they but see and on the other side".

In the Swedish literature from older time there is a report on an even longer, though unsuccessful crossing witnessed in a lake, Siljan, about as broad as Storsjön. From a boat it was observed how lemmings near the north shore "were struggling vigorously in the waves", but 10 km out in the lake a multitude of dead bodies were met with (Söderhjelm, 1832).

In the present case at least a part of the lemmings gathering at the point, had on occasion actually, as was established at the first visit, tried the venture of crossing the lake. That during the second visit, in spite of the perfectly calm weather, none was seen to do this, was surely due to the prevailing mist.

That the animals, when finding the circumstances at the point discouraging, did not stay next to the shore and spend the day in the adjacent forest was explainable by the present conditions of this. It offered no possibilities for them to support themselves, nor could but a limited number have found hiding-places, if they had tried to stay and seek food in the next, thoroughly grazed field.

Instead they night after night went back to the fields and woods higher up in the peninsula. No information was, however, available to indicate what distances were covered during these movements.

If thus the iterated retreats from the shore would be understandable by the local circumstances, this behaviour never the less seems remarkable.

In all accounts of mass movements of lemmings, even the most experienced observers as Collett emphasize the helplessness of the animals when meeting with dangerous situations during their joint forward running with the animals blindly following each other. Arriving at a lake they might of course deviate along its shore, but when blocked up and accumulated at places like this, they have always been found unable to run back on their route and try another issue. Instead they remain irresolute on the spot until at last continuing forwards, regardless of the conditions in the front.

Here on the contrary, the whole mass of lemmings proved capable of accomplishing, and not only once but time after time, in common a reverse movement that implied a postponement of the perilous crossing.

#### *Other observations and reports on the migration*

It was reported that already at the end of July a great accumulation of lemmings had been noticed at Järpen, on the opposite shore of the river there. They had then for a week been seen crossing the river to the east. A similar event had been observed at Mörsil, at the same water system.

For lemmings moving in a eastern direction within the area bordered by, on one side, Lake Kallsjön and the river emptying it, and on the other side the river along the road from the west (see map), it is natural that they at last would be concentrated at the conjunction of the two rivers

just at Järpen, and for animals arriving at the water further to the south, Mörsil offers the easiest place for a crossing.

The further course of these lemmings cannot be stated by any report, but it is likely that, due to influences from the lakes and water courses they were to meet when heading east, at least part of them deviated towards the south and finally arrived into the peninsula of Hammarnäset and so contributed to the great concentration there.

Other lemmings had been seen on the road from the west, especially halfway from Järpen to Storlien, where they were crossing the river to the south side.

When the observer arrived at the district, on Sept. 24th, the migration was still going on. Driving on the main road to the north from Östersund up to Mörsil and Järpen, run over lemmings were encountered in increasing numbers. At the last named places the bodies lay concentrated up to several bodies per square metre. Taking off from the main road and continuing to the north on the east side of Lake Kallsjön, bodies were still met with, though here scarcer. Going back on the same road on Oct. 9th, hardly any were seen, and observations during two later visits confirmed that only a few lemmings could be on the move within the district. But, ten days later numerous lemmings were reported from a place, further to the east, at the mainroad Järpen-Östersund where it crosses another river, and on Oct. 9th the migration past Sundet was, as stated in the foregoing, still in full progress. All this indicated several migration streams of different origin from the north.

Whereas it seems that no lemmings had been observed at the west side of Lake Storsjön, below the peninsula of Hammarnäset, they had later on the east side even entered the town of Östersund and were also present on the islands outside. These animals were probably ones that had started from Hammarnäset and succeeded in crossing the lake, and those found at a place 70 km SE of Östersund at the same water system could be of the same origin. Other lemmings, reported from the eastern part of the province, were signs of other migration streams, which, due to the general direction of the water courses were likely to proceed from NW to SE.

The above localities, did not, however, represent the limits of the great lemming invasion in that year. Later in the autumn there came reports stating that lemmings had reached a place 40 km from the east coast, as well as the town of Sundsvall, situated at the very shore of the Baltic sea and 250 km from the next fell districts. The last time such an extended migration has been reported was, according to Ekman (1944), in the years of 1907 and 1923.

## II. The spring observations

### Observations in the fields at Sundet

The time between the 18th and the 21st of May was devoted to the place studied in the autumn, Sundet, and to the nearest fell area to the north of it, Skäckerfjällen.

In the fields at Sundet no living lemming was now to be found, and very few had been visible when the snow came. Around the middle of April the farm dog had killed half a dozen lemmings around the houses and since then none had been seen.

In one of the fields, where in the autumn a number of the resident lemmings had had their dwelling-places in holes and runways, there were now no signs of winter activity. In this sloping, wind-exposed part of the fields the snow had, as was told, been scanty, periodically thawed and disappeared early. The lemmings had therefore, no doubt, early in the cold season been obliged to move away and find another abode.

An inspection of the holes in the centres of the runway system revealed that some

of them went only straight down, i.e. were left just as when the hurdle pole had been pulled up, though now with some grass on the bottom. In others, the lemmings had from the bottom dug an excavation into the side just deep enough to keep an animal shielded from rain entering the hole. In three cases there was, however, a tunnel descending obliquely for about 40 cm and directed in towards the slope across which the hurdle had been standing. Innermost it had nesting material of grass.

In the immediately adjoining old field covered by tussocky grass, where in the autumn other resident lemmings had had runs and tunnels, there were now clear signs of previous activity under the snow cover. Only a few animals seemed, though, to have been staying there.

Instead, another field in the neighbourhood, isolated from the main field area by a coppice, turned out to be the place where a greater number of lemmings had chosen their winter quarters. It was an old field on dry ground that for many years had not been cultivated.

In the autumn no lemmings had settled there, although migration had occasionally been witnessed on a pathway passing along it towards another field. In the latter with its better grazing a number of stationary lemmings had been dwelling, some of them using the outhouses of a deserted cottage as shelters. There, on the other hand, were now no traces of a later winter activity. The reason why these animals, if they were actually the same ones, had changed over to the present field with the winter quarters could not be stated, though it is probable that the snow cover, due to the more shielded site, had been deeper in the latter.

This field was roughly rectangular in shape with its length axis going N-S. Bordered along its longer sides by leaf-wood and shrubs, mixed with spruce, it sloped gently to the south almost down to the lake arm, while towards its north edge there was an opposite light slant to the north, still with a snow drift, the last remaining one within the whole area of fields.

In this field, overgrown in part with tussocky grasses and scattered saplings of birch and willow, traces left from the winter activity could be seen in the form of winding and branching lines and tunnels of cut grass, indicating the places of previous burrowing under the snow. Beside this, 14 winter nests could be counted within the area.

As such vestiges from the winter activity of lemmings seem to be only cursorily mentioned in literature and some typical features appeared here particularly clearly, they deserve a description.

The grass lines and tunnels had resulted from the lemmings moving on the ground under the snow and digging tunnels through the snow in search of food. As they feed on the basal, still living parts of the grass they, in order to get at these more easily, cut off the withered upper parts of the stems and leaf-blades. This waste material would soon fill the snow tunnels, blocking further passage, but to prevent this the grass had been pressed into the sides and sometimes, too, against the roof. After the thaw the courses of the previous snow tunnels appeared, either as open runways with raised borders of cut grass, or where there had been more of this, as completely covered grass tunnels.

From these runways and tunnels shorter or longer blind alleys branched out here and there, sometimes bulging to what from the outside could be taken for shelters or nests (Fig. 5). These branches were, however, never hollow but entirely solid, composed of firmly packed grass forming true casts of the previous snow burrows. Into these the lemmings, after having used them for foraging, had stowed away grass that had become too bulky in the other tunnels used as passages.



Fig. 5. From a wintering area of lemmings. While foraging under the snow cover, they have dug systems of tunnels in the snow, packing the waste grass against walls and roof. The remaining grass tunnels seen here thus constitute casts of the previous snow tunnels. The roof has been opened to show where it was free passage. From the sides are bulging out blind alleys compactly filled with waste material.

In some spots there could be seen a variant of such waste deposits, demonstrating the process of working. A stretch of a grass runway appeared there divided in a series of compartments, separated by more or less vertical grass partitions (Fig. 6). The explanation of this was probably that while the animals had been filling the passage by pushing before them one mouthful of grass after the other, they had each time also happened to push in front of the grass some of the snow existing in the tunnel, every load thus becoming separated from the previous one by a layer of snow, which after thawing left an empty space.

The winter nests found in the same field as the tunnels described were sometimes situated in connection with these but in other cases not. Nine of them were found within a length of 65 m of the field, which here measured about 25 m across, and some only a few metres apart. Almost all the nests were built entirely of cut grass but two were of grass and *Polytrichum*-stems mixed together. In form they were dome-shaped with the exception of two more oval ones. Two nests were constructed on a somewhat elevated platform of grass but all the others rested directly on the ground. In size they varied and though most of them had a diameter of about 20 to 24 cm, one was somewhat bigger, 24 × 26 cm, and two measured only 13 and 14 cm across. A few of them proved to have two entrances to the interior which in most cases was lined with grass, finer than on the outside. For two nests a grass tussock had been used, a part of which was excavated from a small hole at the side and inside lined in the usual way.

Some other grass tussocks immediately beside feeding-places were found to be treated in a simi-



Fig. 6. From the same place as Fig. 5. The course of previous snow tunnels. The loads of grass packed into them became here during the work separated by snow which after thawing left inter-spaces between the loads.

ar way but were evidently not proper nests, the opening at the side being here much wider so that the whole of the interior, which had no lining, could now be seen from the outside. Tussocks, excavated in this way, had been seen also in the previous autumn, then being used by stationary lemmings as shelters. That the present ones, though, had been gnawn out while covered by the snow was revealed by some cut grass that had been pushed outside the entrance and was now still showing the form of the connecting tunnel (Fig. 7).

Finally, there was another nest found in a big *Polytrichum*-tussock, measuring 1 metre across. From a hole at the side a tunnel, 60 cm long, went towards the middle, ending in a cavity lined with grass.

At two of the nests, some dm from the entrances, there was a heap of droppings placed in a runway. In the vicinity of some other nests there were also found more irregular heaps, which by their form and site indicated that they had originally been placed in a snow tunnel higher up in the snow cover and when this melted had sunk to the ground. As well as this, scattered pellets were lying here and there over the area.

Whether the nests represented the total number of lemmings dwelling within the winter quarters area was not possible to ascertain. Ekman (1907) indicates that a nest may be used by more than one individual. Besides, it was not impossible that other lemmings had shelters among the shrub and herb vegetation on the surrounding ground and from there had come into the field for feeding, but this was not found out.

The prerequisite for the formation of the well-defined grass tunnels remaining after the thaw was evidently the condition of the grass cover in the feeding places.



Fig. 7. From the same area as Fig. 5. Grass tussocks gnawed out by lemmings under the snow cover and used as shelters.

In many places it occurs that the snow does not rest directly on the ground, due to the fact that during its formation the falling snow does not penetrate down to the soil but remains hanging on the upper parts of the vegetation cover. This happens for instance in spots where the latter consists of coarse herbs or long grass remaining more or less erect after the vegetation period. Where the snow is suspended in this way on the vegetation, more or less extensive air spaces remain between its under side and the ground (Formosov, 1946). The importance of this subnivean space for small mammals during the winter, in giving them access to forage ground as well as protection against the cold, is pointed out by Coulianov and Johnels (1963).

It is obvious that in places with subnivean spaces where the lemmings are able to move freely in the vegetation under the snow, the traces from their feeding activity would not take the form of such grass tunnels as described above.

In the present field, on the other hand, the grass between the scattered tussocks was in parts relatively short and had, entirely withered, already in the autumn been lying more or less flat. This was even more pronounced after the thaw and it was obvious that over most of the area the grass had been pressed to the ground by the snow so that no subnivean space was available. The lemmings had therefore not been able to move about within the grass cover but only on the top of it, by making their way through the snow. In some spots, however, the cut grass was lying as a diffuse layer, indicating a previous air space.

As no dead lemming was found within the area the lemming droppings were the only traces proving that the nests had actually been built by lemmings. The smaller

of them would otherwise, by their construction alone, be impossible to distinguish from nests made for instance by field voles (*Microtus agrestis*). During the previous autumn all voles seemed to have been scarce in the district, and at Sundet the only ones observed were some young ones from a litter of field vole living far away from this field.

Subnivean nests, built by lemmings in their natural haunts, are described by several authors (Ekman, 1907; Collett, 1911–12; Hustich, 1935–36; Folitarek in Ognev, 1948; Nasimovich *et al.*, 1948). Collett is of the opinion that most winter nests of this species are subterranean. Formosov (op. cit.) and Koshkina and Khalansky (1963) on the other hand, referring to lemmings and voles, emphasize that while the animals use subterranean nests during the summer, they abandon these in winter and build subnivean nests, which due to the insulating properties of the snow give better protection against the cold than those situated down in the frozen soil.

Tunnels are made also by voles. Formosov (op.cit.) refers to them as "a complicated branching reticulum of bolsters and sausages on the surface of the soil near burrow, consisting of chewed dead leaves, mosses, lichens and soil, left by moles and water voles, common, field (*Microtus agrestis*), rat-headed, red-backed voles, Norwegian lemmings." Arwidsson (1928) describes tunnels of grass and mosses made by field voles.—The observer has elsewhere had opportunities of examining grass tunnels made by field voles during the winter. They looked on an average narrower than those made by lemmings but in general would be almost indistinguishable from the latter ones. It is to be expected that when made by the somewhat larger rat-headed vole (*Microtus oeconomus*) they would be still more difficult to distinguish.

Tunnels and winter nests were, as will be related in the following, found not only in fields. They were also found, both near Sundet and at higher levels up in the fell areas, in sedge and *Sphagnum*-bogs. In the last case the lemmings, though they do not feed on *Sphagnum*-mosses, had in the usual way cut off moss stems along their way under the snow, evidently to get at the sedges, grasses and herbs that were growing more or less scantily mixed with the moss. Due to the weak and spongeous structure of this kind of moss, the lining of the tunnels had after the thaw not retained its form but was lying collapsed as ill-defined lines.

#### Observations in some fell districts

In the spring three fell districts, Flatruet, Skäckerfjällen and Storlien were visited.

From Flatruet it had earlier been reported that during the spring thaw lemmings had been seen moving up the slopes of the fell. One informant had also observed animals on the move from another small fell, separated from Flatruet by a valley with a small river. While keeping a direction to the north, they had first gone downhill and then, after crossing the river, on the other side walked up towards the fell plateau of Flatruet. At the highest point of this plateau, a great accumulation of animals had been found. Coming from lower altitudes the animals had evidently been attracted to this wind-exposed spot as being the only snow-free area. At the time of the observer's visit a number of them were still staying at the place, although this with its stony soil, covered mostly by lichens (*Cladonia* sp.) mixed with patches of scanty moss and with low wind-deformed junipers as the only available shelters, seemed to be a less suitable feeding ground than the adjoining lower parts of the plateau with peat bogs and marshes, where now also other lemmings were found.

Traces of winter activity were found at a lower level in a rather dry birch forest on a slope, but these quarters were at the time abandoned. Instead animals were

found out in open marsh and bog land around the same level. At the border of some small peat bogs in the conifer woods below the fells, feeding traces and droppings in runs revealed that lemmings were dwelling at still lower levels.

On the slopes of Skäckerfjällen, winter quarters and a few nests were found from the conifer woods and as high as ground which at the time was snow-free. Both below and above the tree-limit, marshy areas with mosses and sedge had been chosen for feeding grounds. Runs between tussocks and fresh droppings betrayed that lemmings were still living there but hardly any were seen.

After the thaw lemmings had been numerous at Storlien in the valley below the fell, and early in May masses of lemmings had been seen heading towards the fells at another place situated in the birch forest zone below the same fell complex. Also at Storlien winter quarters, including some nests, were localized at levels from the conifer wood and up above the tree-line, but at the time of the visit lemmings were met with only at the higher levels.

#### *Some notes on the behaviour of the lemmings*

During the three days that Flatruet was visited, only stationary lemmings were seen. Probably because they were not so numerous and the vegetation cover here was uniform all around the highest part of the fell, so that no grazing area could preferred to another, the animals did not appear in flocks as those studied at Sundet in the autumn. The single animals scattered over the place behaved, however, as those in the autumn, exposing themselves quite openly while walking around or sitting and feeding without ever interrupting their occupation for keeping a lookout. Nevertheless, they were rather wary and would react from far off to the observer by running and hiding under the nearest juniper.

As for the lemmings on Skäckerfjällen they had perhaps started breeding; at least they seemed to have adopted the secluded way of living usually noted on the breeding grounds.

On the fell at Storlien, most of the lemmings were stationary ones and behaved as those on Flatruet. Beside these, others were now and then seen which were still on the move. They did not show any haste, frequently stopping to nibble at some food. If approached they would make front and assume the threat posture. By crouching down it was, however, possible to approach some of them rather near without any reaction from them, and filming could be undertaken from about two metres. In connection with this an incident may be related.

Through the field glass a lemming was seen crossing a snow-covered area, about 50 m wide, and then disappearing among the tussocks of a small peat bog. Walking up to this the observer caught sight of the lemming which immediately ran away along a run and hid in a hole in a tussock. This hole was not, as was found later, the entrance of a tunnel but just a shallow cavity. The film camera was put up 2 m from the hole and so placed that the run went straight out from the camera. The lemming soon left its shelter but quickly returned into it when the motor started running. After some tentative starts the animal became accustomed to the noise and remained sitting outside the hole, also accepting a hand in front of the apparatus. Then it turned away and quietly began walking in the run away from the camera. Changing position the observer happened to crack a twig. At the noise the lemming swiftly turned and ran back towards the camera and into the hole. The film had now run out and preparations were made for changing it. During this, by scraping and tapping on the film box, the animal could be made to stay within the hole until all was ready. Then further sequences could be taken, showing how after leaving its hole it ran away.

but, as soon as the noise was repeated, immediately returned towards the camera and into its hole. This performance was repeated half a dozen times, the animal returning even when 3 to 4 m away from the hole.

The incident demonstrated that lemmings may react as readily to noises as to visible signs of danger—in this case the crouching observer not being regarded as a menace. It also suggests why a casual visitor may walk over ground where lemmings have their dwelling-places without ever noticing any animal.

This lemming was probably on the move and previously unfamiliar with the surroundings when it happened to find the hole. There is no reason to believe that it was unable to localize the direction from which the noise came. Without doubt it ran towards the supposed danger on purpose in order to reach the only place that it just before had found to be safe, in preference of trying to find a new shelter.

Similar behaviour observed in lemmings actually on the move on a track is related above (p. 338).

#### **Signs of movements in the woodlands**

In Härjedalen, driving to and from the fell Flatruet morning and night, freshly killed lemmings were daily found on the road, also below the slopes of the fell in the upper conifer wood, though the traffic on this road was far from dense.

In Jämtland, during the trip to the district around Sundet, only a few lemmings were found run-over along the road leading there from the north end of Kallsjön. An observation made in April was reported by some men who had then worked at the bridge over the short stream that, emerging at that lake end, comes from the lake above. At that time, there had in the latter lake only been open water in the parts surrounding the stream, and during one week "a stream" of swimming lemmings had been seen daily, crossing the lake end from the east to the west.

A visit was also paid to Hammarnäset, the site of the great accumulation in the autumn. No living or dead lemming was now seen anywhere but it was reported that earlier, during the thaw, small numbers of lemmings had been seen both in the north part and at the end of the peninsula. Also at Järpen, where lemmings had been observed during the winter, even near to the houses, some animals had still been visible during the thaw.

There was, however, evidence that at the time of the journey lemmings were still on the move in the woodlands also at places well away from the fell districts.

Leaving Härjedalen on the road from Funäsdalen to the east, run-over lemmings were found along a stretch up to 40 km from the next fell. An informant had somewhat earlier found animals still 20 km further on.

In Jämtland, when driving on the road that follows the east shore of Kallsjön, a great number of run-over lemmings were counted. All of them were lying within a stretch of 30 km, where the road after turning sharply continues in a NE direction along the south side of a deep inlet. Into the innermost end of this a short stream emerges from a lake inside the inlet. The contours of the lakes here form a funnel catching animals coming from directions between E and SE. That the animals found on the road had in fact arrived there in this way, was also proved by other circumstances at the places. Going back on the same road three days later, about as many bodies were met with again and at the same spots. Further to the south, between Järpen and Mörsil, where three days earlier no lemming had been seen, scores of fresh bodies were now lying.

On the same day, between Järpen and Storlien, where the road runs through the conifer woodland not far from smaller isolated fells, about as many bodies were counted. Returning two days later, a few newly killed bodies were seen along the same stretch. Further to the east, on the main road between Järpen and Östersund, only a single one was seen 20 km before the town just at the same place where the first ones had been found in the autumn when arriving at the district.

The above observations showed that a movement of lemmings towards the fells had occurred at the north end of Kallsjön, just at the same place where in the previous year in August a crossing in the opposite direction had been noticed. The run-over animals were met with along the same road stretches as had been frequented by lemmings in the autumn. For the animals on the road to Storlien nothing could be stated about the direction from which they had arrived. It was, however, at the same places that a migration to the south had been observed in the previous autumn.

That the lemmings found between Järpen and Mörsil should have come there from the west side of the water, as in the autumn, was highly improbable. In the spring no accumulation on that side had been noticed, and there is all reason to believe that they had arrived at these places from the east, as the animals found further to the north along Kallsjön had done.

#### Discussion

The observations in two of the fell districts showed that after the great migration in the autumn a number of lemmings had stayed behind on the fells. On the other hand there was no means of deciding to what extent the animals found established there in the spring might have included individuals that earlier had come up there after wintering in the woodland below. That some of the animals belonged to the latter category was, as has been related, betrayed by their behaviour.

Available reports agree that where lemmings in the spring had been observed in the woodlands more or less far from the fell areas, this had been immediately after the spring thaw and that they had then soon disappeared. Obviously, as soon as the protective snow-cover thawed in their winter quarters, the lemmings left these and wandered up onto the fell plateaux, even if these at the time, as was the case on Flatruet, were still for the most part snow-covered.

Considering this general early break-up it is understandable that the present observations, made at a later date along the roads, could render only a very incomplete idea of the true extensiveness of the spring movements. Nevertheless, these observations when compared with those from the previous autumn were sufficient to indicate that lemmings had been on the move in the woodlands up to 60 km from the fell country. A population of lemmings that had wintered in the woodland to the east of the water system between Kallsjön and Storsjön had, in the spring, been moving away from their winter quarters. It is notable that where the directions of the animals could be discerned, these directions would actually lead them back into the fell districts. If on the other hand, the movements were merely accidental, i.e. the animals spread out at random in all directions, including the south, one would have expected to observe lemmings on the roads above Hammarnäset, too, and they would, at least to some extent, have entered the peninsula itself, for the same reason as in the autumn.

The circumstances thus indicated that lemmings after wintering in the woodland had started a migration back towards the fell districts. While it is probable that a part of those lemmings that were seen up on the fells had returned there from a merely local movement down into the adjoining conifer woods, the animals moving out from the winter quarters mentioned were returning from what can be considered as a long range migration. As for the other lemmings found on the roads at similar or longer distances, these too, could, of course, have arrived at the spot from still much greater distances. Likewise, nothing can be predicted about what distances these animals would cover further on, before finally stopping and breeding.

Obviously, far from all movements of lemmings in the spring can be ascribed to returns from lower altitudes. It is known that in spring as well as in autumn lemmings within the fell areas may be moving in any direction.

For instance Ekman (1944) mentions this; earlier (1907) he also expressed the view that when two successive peak years occur, the lemmings which, in the first year, have come down into the upper conifer woods and breed there, may continue their wandering further down into the lowlands in the spring of the second year.

In the fell districts of Finland Kalela (1963 and in Koponen *et al.*, 1961) found a regular "seasonal change of habitat" from wintering places at higher altitudes downwards to summer habitats "in the birch region and the lower alpine region".

In older literature the tendency is to acknowledge that emigrated lemmings after wintering at lower altitudes may return to the fells in the spring. However, the evidence available for supporting this view is scanty and in parts somewhat vague.

From Finland Granit (1898) relates some north-directed movements and believes that the lemmings "sometimes" return from the lowland, if they have not come too far from the fell areas.

Collett (1895, 1911–12) is similarly of the opinion that in Norway, of those individuals that reach the bottom of the big valleys or the more open lowlands, few return to the mountains. Only in the arctic parts of the country where fells and lowland are not far apart, as well as in the case of animals which have stayed within the subarctic valleys, return movements have sometimes been noticed.

Pleske (1889), in his treatise on the mammals of the Kola peninsula, writes that when the migrated lemmings have survived under the snow a return is possible, though he does not dare to judge whether this would occur regularly, "as only three observers, Högström, Söderhjelm and Wheelwright speak with certainty of it." As the testimonies quoted by him have their provenance in Sweden they ought to be of special interest for the present question.

From the account of Högström (1749) can be concluded that he himself "in the summer" when "the cold was still prevailing in the fells" had witnessed a return movement at a place Kaitum, in Swedish Lapland. This place is situated about 20 km to the east of the easternmost offsets of the fell range. According to his informants, such returns had also earlier been the custom of the lemmings, though they had been occurring at longer or shorter intervals and undertaken by a highly reduced number of animals, in comparison to the migrants that had previously come down from the fells. Högström wanted to find out how far the lemmings had gone to the east or southeast "before they turned" and later learned that they had appeared also down in the country to the east of the Lapland border, which goes about 100 km from the fells. He is though, not referring to any observations of his own on return movements from any other place than the one mentioned.

Söderhjelm in a report (1832) writes that the lemmings in their haunts "have runs in the snow during the winter" and when the ground sometimes becomes frozen during a long time so that an ice-crust is formed which prevents the animals from getting at their food, this probably causes their emigrations. "It then happens, however, that a part of them change their mind and return to their beloved native country". As an example of this he refers to a received report of an event witnessed at a place Särna in the woodlands some 50 kms to the south of the main mountain range. "Several thousands of lemmings" were passing the place towards the north. Unfortunately nothing is mentioned about which time of the year this had happened. His previous statement suggests that it was while it was still winter up in the fells, but other circumstances in the report could indicate that it was already spring at the place of the event. That Söderhjelm himself did not interpret this as a return after wintering in the lowlands was perhaps due to his view expressed further on that such migrants always "disappear" in the following spring and die away.

Other contributors to the same report only state that the lemmings after wintering in the woodland had "disappeared" in the spring.

Wheelwright's spring observations of migrating lemmings were made in another place in Lapland, Kvikkjokk, which is situated only a few km from the nearest fell slope.

Of the above three reports from Sweden, it seems that Högström's account could, if one accepts his view based on information from the inhabitants, indicate a return movement from far greater distances than from the place where he himself witnessed it. Such as the facts are given in Söderhjelm's report, the event cannot with certainty be used as evidence of a return after wintering, even if this is the most probable explanation. In the case of Wheelwright's observations, it is not possible to state if the lemmings seen had actually been on return from an extended migration or were merely signs of a more local movement.

While in their handbooks of the Swedish fauna both Nilsson (1847), Holmgren (1865) and Lilljeborg (1874), without referring to any sources, state that the lemmings return in the spring, no other observations than those cited above seem to be found in the Swedish literature from older times.

In later literature the existence of such return movements are not taken into consideration. The common view is that in migration years most or all of the emigrated lemmings are condemned to perish and that their only rôle, as Elton (1930) puts it, is to "remove a surplus population from the area usually inhabited by the species".

He also (1942) points out the difficulty of understanding "how evolution by natural selection would have maintained the migratory stimulus when all those that respond to it perish, and those that do not are the survivors".

More recent investigations have, however, proved that in cases the migrations can result in colonization of new breeding areas.

This has been shown by Kalela (1941, 1949 a, b) in the case of Finland and is mentioned by Folitarek (in Ognev, 1943) at the Kola peninsula. As the topographical features of the country inhabited by lemmings in Finland differ from those of the breeding areas within Scandinavia, the prospects of such an issue are, however, not the same for the Scandinavian populations.

In Finland the main fell districts are situated in the northernmost parts of the country. The line between the subarctic (subalpine) birch wood belt and the land below it with its conifer woods goes in an E-W direction. Further to the south there are, however, in the SE part of Finnish Lapland, within this woodland, some small, more or less isolated fells, rising above the conifer woods.

By his studies on the migration years in Finland Kalela (op. cit.) found that those lemmings that had migrated from the northern fell areas into the lowlands in the southwestern parts of Finnish Lapland had all perished, whereas those going to the southeastern parts and reaching the isolated fell areas there, stayed and bred during the following years.

In Norway the country is dominated by mountain districts distributed around several centres. Between them and at the coasts there are lowlands that only in some districts cover greater areas.

In Sweden the fell districts are restricted to its western side and contiguous with the Norwegian fells, the border between the countries mostly following the watershed. Some smaller fells, isolated from the main range by conifer woods, exist, also in Härjedalen and Jämtland, but are situated in the vicinity of it.

Within Scandinavia the country inhabited by lemmings can therefore as a whole, seen apart from some districts in Norway, be considered as covering one contiguous

mountain area, though within this the breeding grounds may be shifting, locally and temporarily. When in some peak years long range migrations occur from this vast area, it would seem that the prospects for those animals that during their wandering come to remain on the Norwegian side of the watershed, could be somewhat more favourable than is predicted by Collett (*op. cit.*). Due to the topography of that country the chances of coming within reach of suitable breeding grounds after the winter ought to exist at many places, even if this has not been possible to establish by direct observations.

For the lemmings descending the Swedish side of the fell area, i.e. all animals wandering in directions between NE and SW, it is inevitable, though, that by proceeding in these directions they arrive in the woodlands where they, except at a few places, have no chance of reaching any suitable habitat.

As a result of the topographical conditions it would then follow that when the lemmings in migration years spread out, their fate depends on which direction is taken. The animals descending the slopes of the Swedish fells would according to the common view perish, whereas of the populations remaining within Norway, at least part would have a chance of surviving. Within the Scandinavian populations the "migration stimulus" could then be carried on by the latter ones.

If an explanation of the problem pointed out by Elton could be looked for along these lines, an additional possibility is suggested by the present observations, i.e. that there is after all reason to consider again the older view related above. To this further support might be furnished by some reports from more recent time.

Of the peak years of this century only a few are known to have resulted in more extensive migrations. For the years 1907 und 1923, when, as related, lemmings even reached the Baltic coast, no further observations have been published.

However, Rendahl (1942) gives the results of an inquiry from the peak years of 1941–1942, on the occurrence of lemmings. The reports gave evidence that lemmings had appeared at many places in the lowlands, including some localities more than halfway to the Baltic coast. Discussing the observations the author only considers movements directed downwards into the woodlands. Among those of the reports cited that give observations of lemmings in the spring, there are, however, three in which the informants were able to state the directions of animals actually seen on the move. They refer, it is true, to places only up to 10 km from the next fell plateau, but the directions were such that would lead the animals towards the fells.

With the above indications from previous migrations and the present observations and reports as a background, the possibility of more or less regularly occurring returns to the fells by lemmings having wintered in the lowlands seems to be worth taking into consideration. It is evident that such movements undertaken by animals wandering singly and, apart from special occasions, imperceptibly through a wooded and sparsely inhabited country, easily can have been overlooked, especially as peak years resulting in migration have occurred only at long intervals.

It can be assumed that within the progeny of a peak year, highly varying stages of physical fitness are represented. Even if only a small fraction of the numbers of migrants were able to return to their normal haunts, the addition of such individuals, having withstood the hardships of two migrations and a winter between, would obviously imply an enhancement of the viability within the breeding populations of the years to come and would thereby render a survival value to the migration phenomenon.

Further observations in migration years are, however, needed for a final judgement of the question.

#### S U M M A R Y

In the late summer and autumn of 1963 an unusually great emigration of Norwegian lemmings took place down into the woodlands of the adjoining provinces of Jämtland and Härjedalen.

Most of the present observations were carried out between Sept. 24 and Oct. 9 in the district around a farm, Sundet, situated in the conifer woodland about 7 km from the next mountain area.

Across the fields of the farm wandering lemmings were passing in great numbers, most of the animals running on a narrow migration track, formed by their trampling and leading along a field border near and parallel to the lake shore below.

The migration on this track went on during the whole observation period, mainly at night but also regularly by day, and was controlled daily. Counts on peak nights gave numbers up to 35 lemmings passing per minute; in the mornings the highest number attained was 10. Some figures of the variation of the intensity are discussed.

During their wandering on this track the lemmings made, always on the same spots, some deviations from their main direction, and during the whole period the newcomers rigidly kept to the same pattern at these points of their route. Their behaviour at one point is suggested to be a result of their reluctance to proceed towards the water surface suddenly visible in front of the track. Still, simultaneously a cross-wise directed migration could be witnessed that implied swimming over the same lake arm. Likewise incidents at other places showed that the migrants were ready to cross at least smaller water sheets even when this could easily have been avoided.

Even in full daylight the migrants within the area were heading on without the slightest sign of vigilance and showed no reluctance to expose themselves out in the open fields. Likewise the courses taken on tracks or paths did not reveal any attempt to choose routes that would provide any kind of sheltered stretches. They were also seen wandering, not only on gravel roads in the woods but also along the middle of a tarmac highway along a lake shore.

The migrants entirely ignored an immobile observer standing on the track and would walk between his feet in passing. They readily reacted, though, to movements of the observer, this, as was found, at distances of, from the front 15–16 m and from the side 30 m.

The absence of their natural shyness during their migration and their mechanical running on the migration tracks marked out by their predecessors are seen as time- and energy-saving adaptations, of importance for the accomplishment of long range migrations.

At places where the migrants were not travelling on paths or migration tracks, their way of moving appeared equally unhesitating and purposeful, and this whether another lemming was within sight or not. Each individual was carrying through its wandering independently of other migrants, and this must be considered as the normal way of migration in lemmings.

Observation on lemmings swimming in both directions over a lake arm suggested that their course during the crossing was determined by the aid of visual stimuli mutually influencing the swimmers. For lemmings wandering on land such influences could not be stated, except under the special conditions of a mass concentration referred to below.

Some of the migrants arriving at the fields would make a temporary rest to feed. When such animals were approached they would frequently show the well known threat posture. Some of them, however, instead of making front or running away, sank down on the spot and assumed a crouching posture bearing a striking resemblance to that of young waders under similar circumstances. This behaviour, with the animals lying exposed in the stubble of the fields, was observed in daylight as well as at night.

Besides the lemmings passing through the area, there was also a considerable number of other stationary animals to be found, mainly in the fields it seemed but also in the woods around. Feeding out in the open fields in daytime without any sign of vigilance they appeared as unconcerned about the surroundings as the wandering animals. Being familiar with the place they never as-

sumed the threat posture when approached but silently ran and hid in available shelters. Among these stationary animals, two particular categories could be distinguished, here called the gregarious and the resident lemmings.

The gregarious lemmings were found only in the fields and appeared as groups of about 6–20 individuals, each group with a common hiding-place to which the animals regularly retreated from their feeding ground. The causes of these aggregations were evidently the preference for certain types of vegetation on their feeding ground, clearly manifested by the animals, and the lack of natural ground within reach that could offer occasional shelters anywhere. This had induced the animals to share the few, mostly artificial shelters such as piles of hurdle poles or planks, available in the fields or at their borders. As far as was stated, the gregarious lemmings kept inside their shelters at night.

The resident lemmings were, contrary to the rest of the stationary animals, adult specimens that had settled down as solitary dwellers and were found both in the fields and in the woods around. Each of them had a burrow from which a runway system radiated out. All the burrows had a heap of droppings nearby, while none such was found at the shelters of the gregarious animals. In the cultivated fields the holes from removed poles were used as burrows and in some cases a niche or a short tunnel had been dug out at their bottom.

Some data on a small sample, taken among the wandering and stationary lemmings, are given. Among the animals on the move, some bigger ones appeared now and then, but the bulk of them were small specimens weighing less than 50 g and with juvenile uterus or testes. Excepting the residents, the stationary animals were of the same size and status as the latter ones. Apart from one resident animal in early pregnancy, the adult ♀ showed a regressed uterus with placental scars.

A few small young ones aged between 2 and 3 weeks were the only proofs of breeding found in the district.

Some observations on an unusually great concentration of lemmings at a lake in another district are given. Lemmings on the move that had accumulated within a peninsula were, during the day, dwelling in the fields and woods within it. At night they wandered down to the very point of the peninsula where the animals formed a dense mass literally covering the ground. At dawn all the animals withdrew again from the shore to the country above. This behaviour, evidently due to the unfavourable conditions for proceeding over the lake, had even before the arrival of the observer been repeatedly witnessed for some time. It seems to reveal a greater faculty of counteracting a dangerous situation than is generally credited to lemmings on migration.

From reports it was stated that during the autumn lemmings had not only appeared in the eastern parts of Jämtland but even reached the coast of the Baltic sea. Thereby these animals had achieved a migration covering at least 250 km, as counted from the next mountain districts.

In the spring of 1964 the fields at the farm were visited again and the traces of the lemmings' winter activity studied. Subnivean grass nests and systems of remaining grass tunnels within a winter area are described and the prerequisites for their formation discussed.

Some mountain areas were visited and observations revealed that lemmings had wintered from down in the adjoining conifer woods and up above the tree-line. Lemmings were at the time also present at these altitudes, at one place animals still on the move were crossing the mountain plateau.

From received reports and by counting run-over lemmings along the roads in the woodland districts visited, it could be stated that movements within these had been observed earlier just after the spring thaw and were to some extent still going on, up to 60 km from the mountain areas. It indicated i.a. that a population of lemmings had wintered within an area situated up to 50 km from the next mountain country, and that animals from this area in the spring were actually on the move back towards the mountains.

Discussing this the possibility is brought up that such a return migration, contrary to common belief, might be a more or less regular, though due to the difficulties of observing it, easily overlooked phenomenon.

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